



Flowers of Araliaceae: structural diversity, developmental and evolutionary aspects

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With 37 figures

Abstract

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Within Araliaceae, at least four groups are recognized to have significant deviations from the typical euasterid flower groundplan: (1) Asian *Schefflera* clade (incl. *Tupidanthus*), (2) *Plerandra* group, (3) *Tetraplasandra* and (4) *Osmoxylon*. The main trends of flower structure variation are: reduction of calyx, increase in number of stamen whorls, increase of overall flower merism or only of stamen number, increase or decrease of carpel number, congenital petal fusion with postgenital corolla closure into a massive calyptra, appearance of flower disymmetry or asymmetry during flower development or even from its very beginning. Loss of polysymmetry is strongly correlated with increase of organ number, at least in the androecium and in the gynoeceium. Other trends show mosaic distribution between taxa studied. Our data suggest primitiveness of pentamerous tetracyclic polysymmetric flowers (possibly with dimerous gynoeceium) in Araliaceae and multiple losses of this floral construction in the evolution of the family. Multistaminate and multicarpellate flowers are clearly derived types in Araliaceae.

Keywords: Apiales, Araliaceae, flower polymery, flower groundplan, evolution.

Introduction

Araliaceae is a family of euasterids II (APGII 2003) closely related to Umbelliferae. This relationship was stated by many researchers on the basis of morphological data (e.g., Bentham & Hooker 1863, Wettstein 1924, Hutchinson 1959, Melchior 1964, Takhtajan 1966, 1987, Cronquist 1981, 1988) and supported by molecular phylogenetics (e.g. Plunkett et al. 2004a). These two families represent the vast majority of species in the order Apiales sensu APGII (2003) and Plunkett et al. (2004a). As well as for many other eudicots, polysymmetric tetracyclic pentamerous (often except the gynoeceium) flowers are considered to be typical for Apiales. In contrast to many other asterids, presence of a corolla tube is rare in Apiales. Umbelliferae are generally charac-

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terized by low variation of mature flower structure (e.g., Drude 1898, Erbar & Leins 1997, Leins & Erbar 2004), that is why systematics of this group was mainly based on fruit morphology and anatomy (e.g., Hoffmann 1814, Drude 1898). As pointed out by Cronquist (1981), “all of the features that have been used to distinguish the Apiaceae as a family can be found individually in Araliaceae”. This is evidence of their closest relationships and the reason of difficulties with delimitation of these families (Baumann 1946, Pervukhina 1953, Tikhomirov 1961, Plunkett et al. 2004a). In contrast to Umbelliferae, flower morphology of Araliaceae is extremely diverse; moreover, many species of this family possess flowers that are unusual for euasterids due to their remarkable variation in merism and other crucial characters of the flower groundplan (Harms 1898, Melchior 1964, Philipson 1970, Eyde & Tseng 1971). Floral morphology of these species of Araliaceae caused a discussion on the ancestral flower structure for the order Apiales (reviewed in Eyde & Tseng 1971).

Before the middle of the XXth century it was commonly accepted that the higher the number of elements in the flower, the more primitive it is. Hence, most of the araliaceous genera with polymerous flowers (*Tetraplasandra*, *Plerandra* and *Tupidanthus*) were grouped together and put at the base of the family Araliaceae and the order Apiales (or Umbellales in Li 1942). Cronquist (1968, 1981) was the first to consider polymerous araliaceous flowers as derived from pentamerous ones. Eyde and Tseng (1971) suggested that the ancestral flower of Araliaceae was slightly polymerous and most of Araliaceae were evaluated to have pentamerous flower, while several genera, e.g. *Plerandra*, *Tetraplasandra* and *Tupidanthus*, underwent secondary polymerization. Takhtajan (1997) fully agreed with Cronquist in the statement that polymerous types probably underwent a secondary increase in the number of parts, but pointed out that polymerization occurred basically in the archaic genera of the family, such as *Tupidanthus*, *Schefflera* and *Tetraplasandra*.

Molecular phylogenetic data (Wen et al. 2001, Plunkett et al. 2004b) support the idea of secondary origin of polymerous flowers within Araliaceae. Mapping of flower merism on the molecular phylogenetic tree shows that species with polymerous flowers are scattered among species with pentamerous flowers. This means that flower polymery appeared independently several times within the family. However, the evolutionary pathways that led to such an unusual phenomenon are still unclear.

The present study is focused on the structural diversity of polymerous flowers within Araliaceae. We compare different evolutionary lineages within this family to understand differences in patterns of variation of different features of flower architecture. Furthermore, we are interested in elucidating possible correlations between variations of different characters.

We have examined three groups of Araliaceae which are remarkable in their polymerous flowers. The first group is the so-called Asian *Schefflera* clade (Plunkett et al. 2005), a monophyletic group of Asian (and some Australian) species of a huge polyphyletic genus *Schefflera* and some segregate genera, such as *Tupidanthus*. This clade includes many species with ordinary pentamerous flowers as well as several taxa with polymerous flowers (e.g., *Tupidanthus*). According to molecular phylogenetics, *Tupidanthus calyptratus* is closely related to *Schefflera subintegra* (M.S. Nuraliev, G.V. Degtjareva et al., unpubl. data). This species with polystemonous (16–27 sta-

mens) flowers was formerly placed in a separate genus *Scheffleropsis* that is most similar to *Tupidanthus* in its floral morphology (Grushvitsky & Skvortsova 1973). *Schefflera actinophylla*, another close relative of *Tupidanthus*, belongs to the *Brassaia* group of *Schefflera*, which is also characterized by polymerous flowers (their merism varies from 10 to 30 — Frodin 1975).

The second group is the genus *Tetraplasandra* that is interesting for its polymerous androecium and variable (inferior to superior) ovary position. According to the molecular data, *Tetraplasandra* is nested within the *Polyscias* s.l. clade (Plunkett et al. 2004b). *Tetraplasandra gymnocarpa* is the only species of Araliaceae with a fully superior ovary. Such an unusual ovary position for Apiales is derived from the (semi)inferior condition (Eyde & Tseng 1969, Costello & Motley 2004). Costello and Motley (2004) found that the ovary becomes superior only at the latest stages of flower development, whereas earlier the ovary resembles that of *Tetraplasandra* species with (semi)inferior ovary. Moreover, a polymerous androecium of two whorls has been reported (Lowry 1990) at least in two species of *Tetraplasandra* (*T. waialealae* and *T. waimeae*).

The third group examined here is the genus *Plerandra* which is remarkable by its numerous stamen whorls. As recent molecular phylogenetic studies show, *Plerandra* is placed in the Melanesian *Schefflera* clade (Plunkett et al. 2004b, Plunkett & Lowry 2008). Whereas most species of this clade belonging to the informal subgroups “*Cana-coschefflera*”, “*Gabriellae*” and “*Dizygotheca*” share pentamerous flowers, the members of *Plerandra* and the closely related subgroup “*Dictyophlebes*” show an increase in number of the androecium whorls from one (*Schefflera costata*, *Plerandra bakeriana*) to seven (*P. pickeringii*) together with increase of the stamen number in each whorl. As a result, the flower of *P. pickeringii* contains up to 500 stamens (Smith & Stone 1968); this is the most extremely polystemonous androecium within euasterids.

Material and methods

Gross morphology and development of flowers for the following species have been examined: *Schefflera venulosa* (Wight & Arnott) Harms (collected from cultivated plants in Tsitsin Main Botanical Garden of the Russian Academy of Sciences, Moscow, in 2005, and in Komarov Botanical Institute, St.-Petersburg, in 2007 and 2008); *Schefflera octophylla* (Loureiro) Harms (collected in Fairy Lake Botanical Gardens, Shenzhen, China, in 2005); *Schefflera actinophylla* (Endl.) Harms (collected from cultivated plants in Fairy Lake Botanical Gardens, Shenzhen, China, 2005, and in Johannesburg, South Africa, 2007); *Tupidanthus calyptratus* J.D. Hooker & Thomson (collected by A.L. Takhtajan and Le Kim Bien, no. 8423 on 19.01.1975 in the province Lai Chau, Vietnam, and from plants cultivated in San Diego, California); *Tetraplasandra waialealae* (collected by David H. Lorence no. 9542, 04.04.2007 in Kauai, Hawaii); *Plerandra insolita* A.C. Sm., *Plerandra grandiflora* A.C. Sm., and *Plerandra victoriae* Gibbs (collected by Gregory M. Plunkett [his voucher' numbers 1834, 1939, 1909 correspondingly] in 2005 in Fiji).

Flowers at various developmental stages were fixed in FAA or 70% ethanol and stored in 70% ethanol. For scanning electron microscopy (SEM), parts of inflorescences and flowers were dehydrated in 100% ethanol and 100% acetone. Dehydrated material was critical-point dried and sputter-coated with Pt/Pd. For light microscope observations, material was sectioned using standard methods of paraffin embedding and serial sectioning at 15 µm thickness (Barykina et al. 2004). Sections were stained in picroindigocarmin and carbolic fuchsine (Axenov 1967) and mounted in Canadian balsam.

Results

Asian *Schefflera* clade. We distinguish four main types of flower groundplan within this group:

1. Many *Schefflera* species from this group including *S. venulosa* (Fig. 1–6) possess typical araliaceous flowers which are tetracyclic, pentamerous, with semi-inferior ovary. Elements of the adjacent whorls alternate with each other (Fig. 1, 3). Flowers typically consist of five inconspicuous sepals fused congenitally at their bases, five free petals with apices curved down toward the gynoecium, five stamens and five united carpels that form an asterisk-shaped compitum (Fig. 19).

2. In *Schefflera octophylla* (Fig. 7–12), flowers differ from typical araliaceous flowers in some crucial characters. In mature flowers, calyx is well-developed and forms a massive tube with short free lobes (Fig. 9, 12). The gynoecium is polymerous and usually consists of 8 (6 to 9) carpels. The style is slightly elliptic rather than circular in cross-section (Fig. 7–10). Although the merism of the gynoecium is increased, the calyx, the corolla, and the androecium form three regularly alternating pentamerous whorls.

3. *Schefflera actinophylla* (Fig. 13–18) usually possesses 12-merous flowers. Merism of different whorls within a flower is not necessarily equal. The calyx is represented by a thin rim at the upper receptacle edge and clearly visible only in SEM images (Fig. 17, 18). In mature flowers, this rim is absolutely homogenous and bears no traces of sepal apices. Unfortunately, we did not study calyx development because of the absence of appropriate material. Another unusual feature of the *S. actinophylla* flowers is a change of symmetry in the course of flower development. In the beginning of flower development, the receptacle is clearly circular in outline (Fig. 13, 14). After elongation of the symplicate zone, however, the carpels in some flowers do not appear to be equally spaced from the flower centre. Rather, they are arranged in two rows along a line, so that the top of the gynoecium is elliptic in cross-section in the mature flowers (Fig. 16). This pattern of carpel arrangement results in a modified elongated shape of pollen tube transmitting tissue in cross-section at the level of the compitum (Fig. 20). The whole flower usually also becomes slightly elliptic in outline. Similar to the carpels, the petals are arranged in two rows along a line in a flower bud viewed from the top (Fig. 15). As a result, the mature flowers are weakly disymmetric. The plane of the flower symmetry is randomly oriented in relation to flower position with respect to its subtending bract and the main axis.

4. The flower structure of *Tupidanthus calyptratus* is described in detail in Sokoloff et al. (2007). The flower is peculiar in its incredibly high merism of gynoecium and androecium (up to 200 elements in each whorl; Grushvitsky 1981, Wen et al. 2001), folded butterfly-like shape of receptacle, which is recognizable from the earliest stages of floral development, and carpels arranged along a branched H-shaped or more complex pattern (see Fig. 1–69 in Sokoloff et al. 2007). The calyx forms an inconspicuous rim. The corolla forms a tube in which no evidence of petal boundaries can be traced. It is initiated as a continuous rim and its vasculature does not allow determining petal number (Nuraliev et al., 2009). Hence, there is no method available to distinguish petals from each other and to establish corolla merism of *Tupidanthus*. The orifice of the

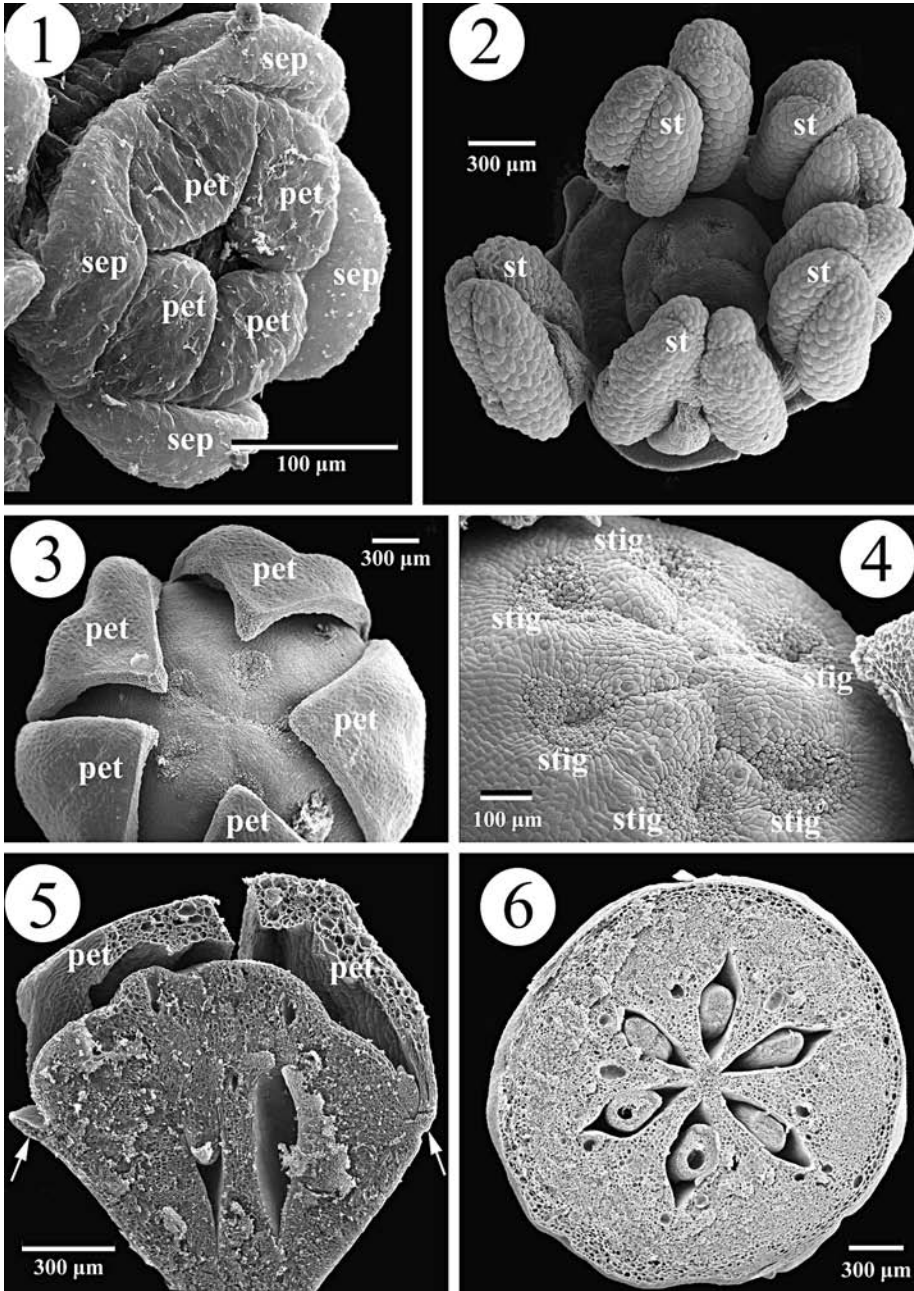


Fig. 1–6. *Schefflera venulosa*. This species typically possesses pentamerous flowers. As in some other species of *Schefflera*, flowers of *S. venulosa* are either hermaphroditic or functionally female (Nuraliev et al. 2009). — 1, Young flower with young sepals and petals, a rare case of a tetramerous flower. — 2, Almost mature hermaphroditic flower, corolla removed. — 3, Mature functionally female pentamerous flower. — 4, A rare case of hexamerous gynoecium in a functionally female flower. — 5, Longitudinal section of mature functionally female flower with visible calyx (arrows). — 6, Transversal section of a six-loculed ovary. — pet = petal, sep = sepal, st = stamen, stig = stigma.

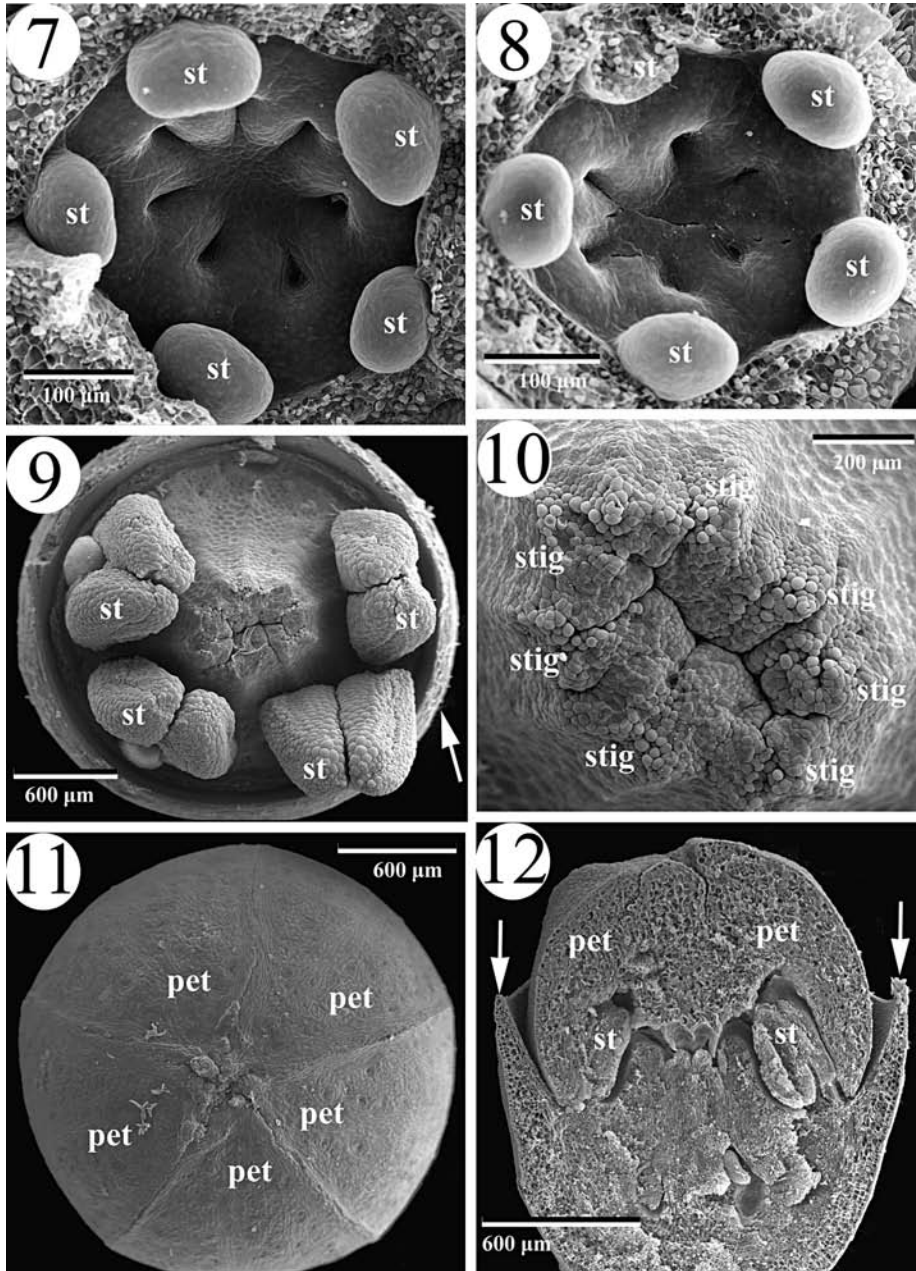


Fig. 7–12. *Schefflera octophylla*. This species is characterized by pentamerous perianth and androecium and polymeric gynoecium. — 7, Young gynoecium of 7 carpels. — 8, Young gynoecium of 6 carpels. 9, — Mature flower, corolla and one of the stamens removed; note the well-developed calyx tube (arrow). — 10, Mature stigmas. 11, Mature corolla, top view. — 12, A longitudinal section of mature flower; note the calyx tube (arrows). — pet = petal, sep = sepal, st = stamen, stig = stigma.

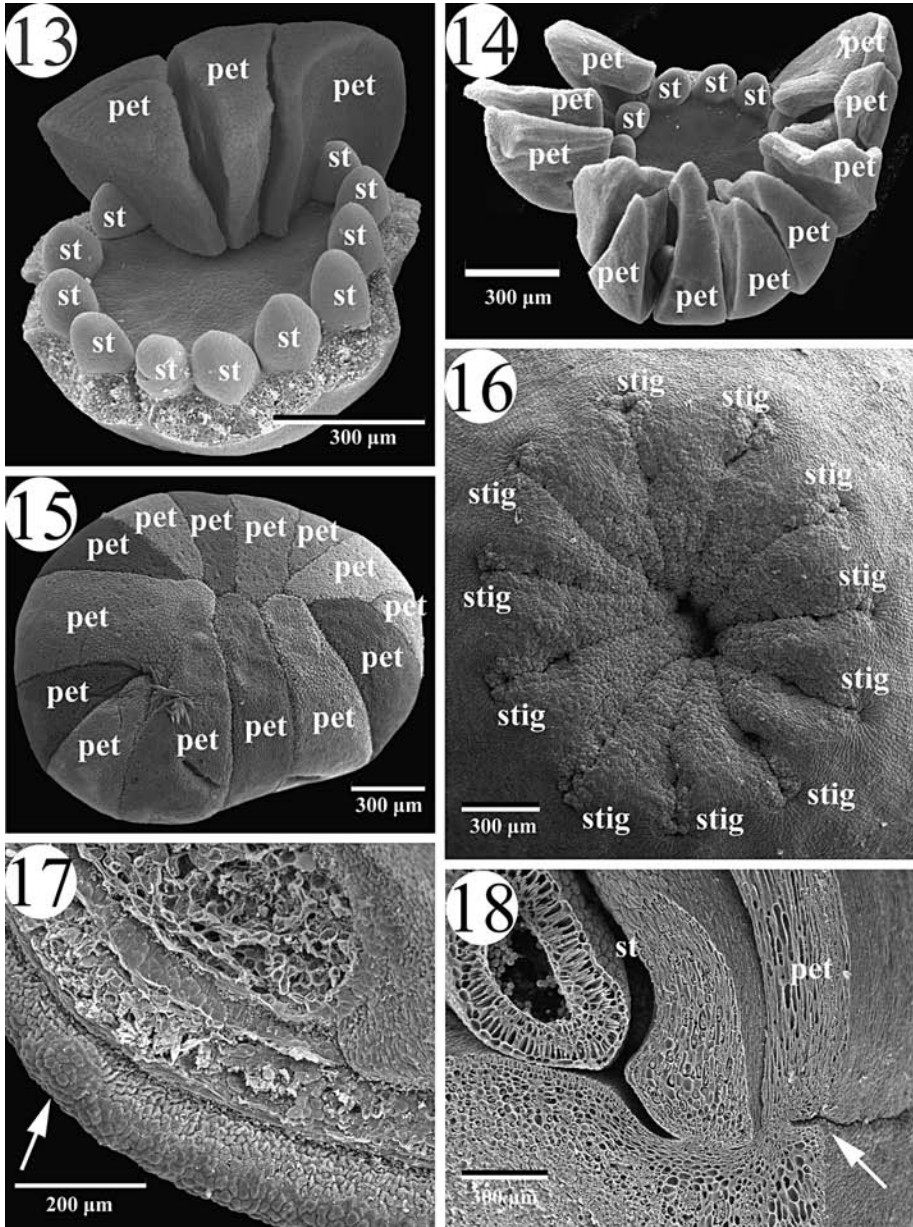


Fig. 13–18. *Schefflera actinophylla*: polymeric (hemi)isomerous flowers. — 13, Young flower at the beginning of gynoecium development, corolla partially removed; note the receptacle is circular in outline. — 14, Flower at slightly later stage; note numerous free petals. — 15, Almost mature corolla in top view; petals tend to meet each other along a line. — 16, Mature gynoecium; carpels meet each other along a line. — 17, Mature calyx (arrow), a petal and a stamen are removed. — 18, A longitudinal section of mature flower; note the inconspicuous calyx (arrow) at the base of the corolla. — pet = petal, st = stamen, stig = stigma.

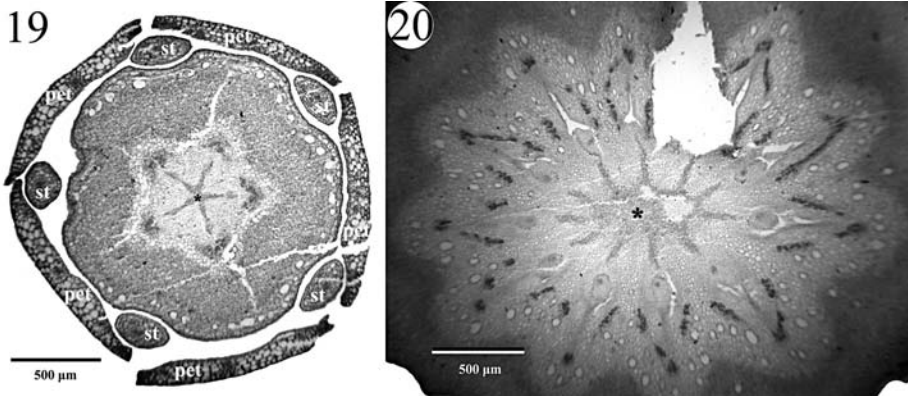


Fig. 19–20. Cross sections of mature *Schefflera* spp. flowers at compitum level (asterisks). — 19, *Schefflera venulosa*, compitum is star-shaped. — 20, *Schefflera actinophylla*, compitum is oval. — pet = petal, st = stamen.

congenitally developed corolla tube postgenitally closes, and the corolla forms a thick calyptra.

It is important to note that in the Asian *Schefflera* species the flower merism is often variable at infraspecific level. For example, in *S. venulosa* we observed several tetramerous and hexamerous flowers. The merism of *S. actinophylla* flowers varies from 11 to 14. Highly polymeric flowers of *T. calyptratus* can bear 50 to 130 (200) stamens and carpels.

Flowers of *Tetraplasandra waialealae* (Fig. 21–30) possess a polymeric androecium combined with oligomerous corolla and gynoecium. Our material does not allow examining the sequence of organ initiation, but contains some relatively early stages with very young carpels and stamens. The calyx of *T. waialealae* forms a relatively massive but shallow cup with almost entire margin (Fig. 21, 28). Precise counting of sepals is problematic. Petal number varies in our material between six and seven (Fig. 21, 26, 28–30). In some flowers, a petal is much narrower than the other petals. Petal aestivation is valvate. The petals are initiated as separated primordia, which fuse postgenitally by their margins in the course of floral development. The petals of young flowers are massive, with tips curved inwards (Fig. 30). Petal tips are in close contact with the young gynoecium in flower buds, and the space allowed for packing young stamens is clearly visible as an undulating furrow in the inner side of a removed corolla. In anthetic flowers the petals are expanded separately forming no calyptra.

At least 28–46 stamens are arranged in a single whorl. The one-whorled condition is especially clear in the youngest flowers (Fig. 21, 22, 24, 25, 27, 28). Stamens inserted on the radii where adjacent petals join each other (alternipetalous stamens) are just slightly more distant from the floral centre than the antepetalous stamens and the shape of stamen whorl appears to be wavy (Fig. 21, 26). Probably, such arrangement of stamens is caused by the shape of the petal bases, which are thicker in their middle parts than near their margins. The number of the antepetalous stamens located in front

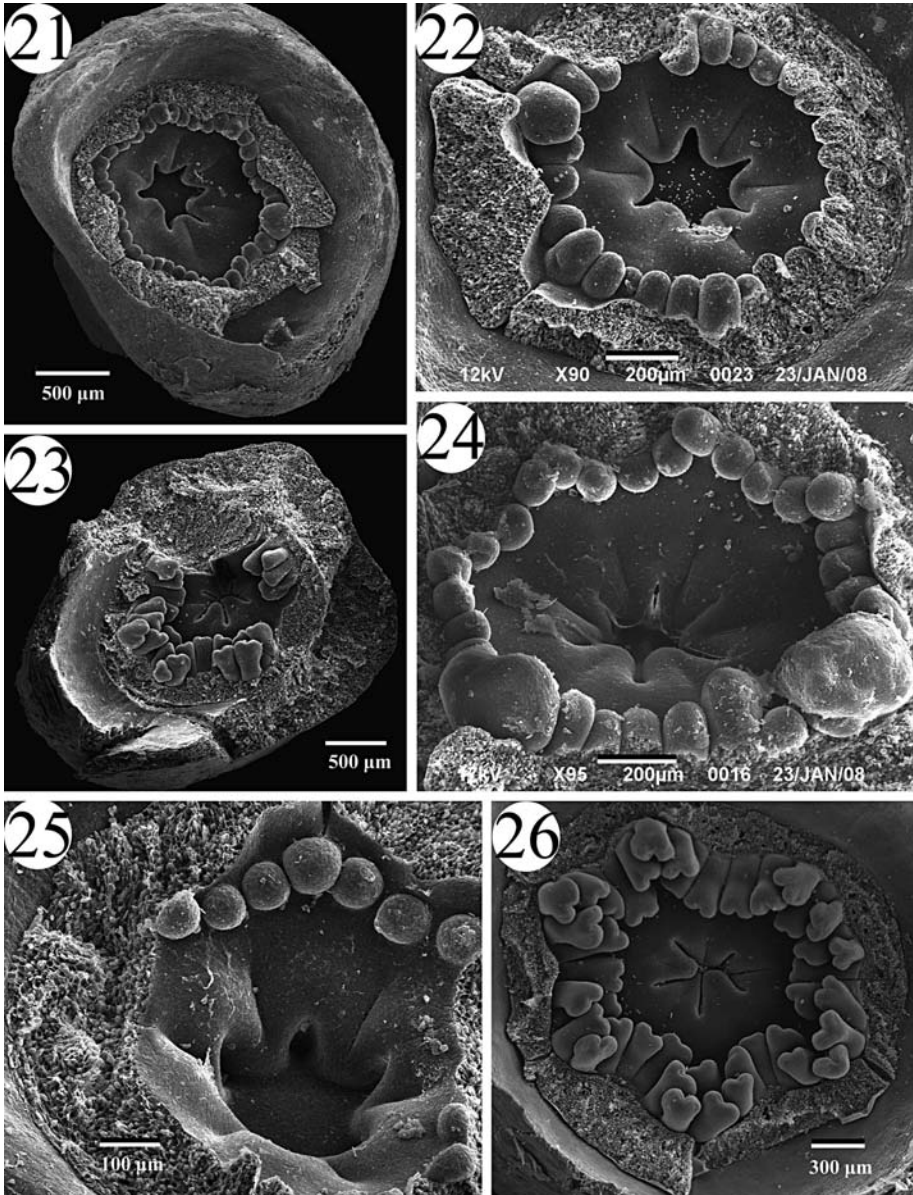


Fig. 21–26. *Tetraplasandra waialealae*: flowers with polymeric androecium. — 21, Developing flower with corolla removed. — 22, Developing androecium and gynoecium; note carpels alternating with petals. — 23, Developing flower with corolla removed, the androecium whorl is folded. — 24, Developing flower with one distinct stamen whorl, note two of six alternipetalous stamens are very large. — 25, Developing gynoecium and part of androecium; note the upper carpel clearly alternates with petals. — 26, Developing flower with corolla removed, the androecium whorl is folded.

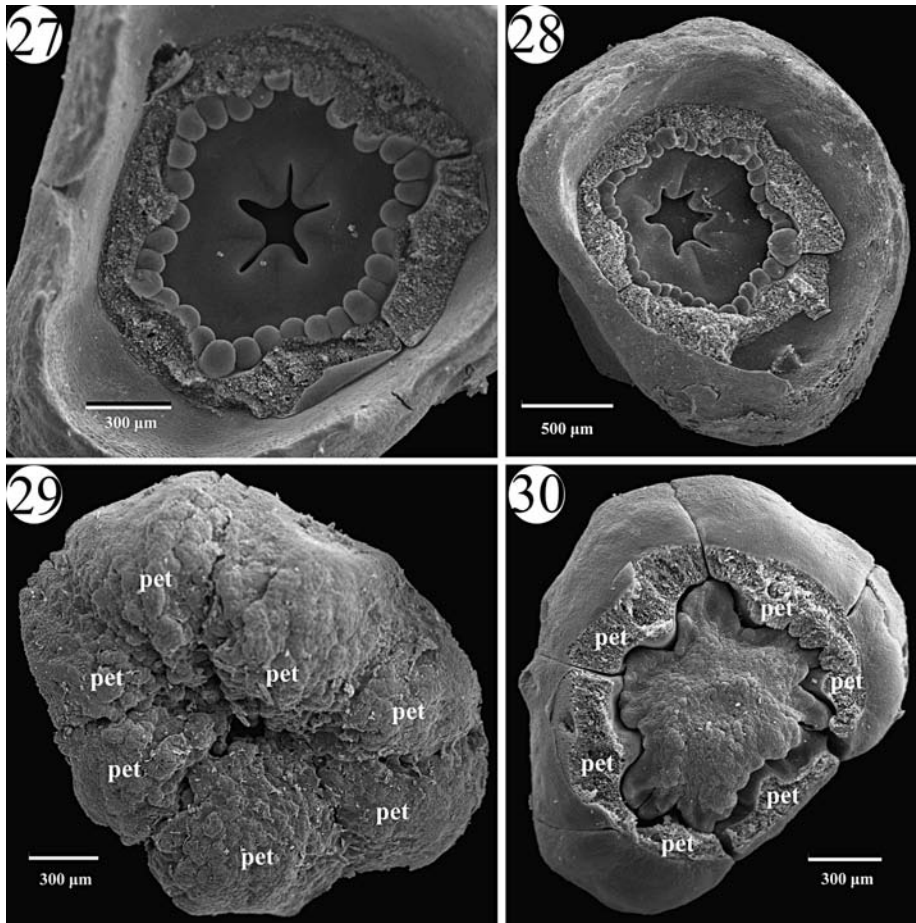


Fig. 27–30. *Tetraplasandra waialealae*. — 27, Developing flower with corolla removed and pentamerous gynoecium. — 28, Developing flower with corolla removed; carpels neither alternate with petals nor are strictly opposite the petals. — 29, Almost mature corolla in top view. — 30, Almost mature corolla in inside view, note the involute petal apices. — pet = petal, stig = stigma.

of a petal is not stable and can vary within a flower (minimum number is two). At early stages before thecal differentiation, the alternipetalous stamens are often larger than the antepetalous ones (Fig. 24). It is tempting to explain this by the fact that the alternipetalous stamens are first to initiate during the androecium development. In some young flowers, however, only few alternipetalous stamens are large, whereas others are of the same size as the antepetalous ones. Occasionally, some of alternipetalous stamens are extremely large (up to six times larger than other stamens); these cases are probably abnormalities in stamen development.

At later developmental stages, the androecium whorl becomes considerably crowded in a waveline (Fig. 23, 26). The number of outer and inner bends is equal to petal

number, with alternipetalous stamens occurring on the tip of the waveline. Apart from folding of the entire whorl, the anthers of the adjacent stamens overlap each other because the anthers are wider than the space allowed for a stamen. This gives the false impression of more than one androecium whorl.

Carpel number varied in our material between five and seven (Fig. 21–28). When carpel number was the same as the petal number (which was not always the case), the carpels occurred either in the same radii as the petals, or in the radii alternating with those of the petals.

A remarkable feature of *Plerandra* (Fig. 31–36) is a concave, cup-like receptacle (Fig. 31, 32). In contrast to the presence of polymerous whorls (i.e., with more than five elements) in androecium and gynoecium, the perianth of *Plerandra* is oligomerous, at least in the examined species. The calyx is typically pentamerous, with sepal bases united in a more or less pronounced tube. Five valvate petals are massive and coherent in young flowers; they expand separately in anthetic flowers, forming no calyptra.

In *P. insoluta* and *P. victoriae*, the flowers bear three whorls of stamens with about 30 stamens in each whorl and one whorl of ten carpels (Fig. 33, 36). Flowers of *P. grandiflora* bear two whorls of stamens with 20–25 stamens in a whorl and a gynoecium with eight or nine carpels (Fig. 34, 35). The outline of each stamen whorl sometimes can be slightly wavy (Fig. 33). Adjacent stamen whorls can slightly differ in the number of stamens in *Plerandra*. Initiation of the stamen whorls proceeds on the concave receptacle in basipetal (i.e., morphologically centripetal) sequence. Alternating stamen position in adjacent whorls was not always obvious. At least in some cases, adjacent stamens of different whorls were clearly on the same radius.

Discussion

Trends in the variation of flowers of Araliaceae

Looking over the variability of araliaceous flowers described above, the following trends in variation in the flower groundplan can be recognized:

1. Variation in whorl number.

(A) Reduction of the calyx up to its complete loss. A well-developed calyx (such as in *Schefflera octophylla* and in species of *Plerandra*) is not common within Araliaceae. Usually, the calyx is much smaller than the corolla; it can form a short tube with free sepal apices (most of *Schefflera* species). In most polymerous flowers, (e.g., in *Osmoxylon* (Philipson 1979), *S. actinophylla* and *T. calyptratus*) the calyx is represented by an inconspicuous rim with no traces of sepal apices. Thus, there is an apparent correlation between flower polymery and calyx reduction. However, the calyx is absent (from the earliest developmental stages) in pentamerous flowers of *Hydrocotyle* (Erbar & Leins 1985). Furthermore, this feature can be found among Umbelliferae and even among its subfamily Apioideae with remarkably stable flower structure, for instance, in the genus *Chaerophyllum* (Erbar & Leins 1997, Leins & Erbar 2004, Sokoloff et al. 2008).

(B) Increase in number of stamen whorls constantly occurs in different species of

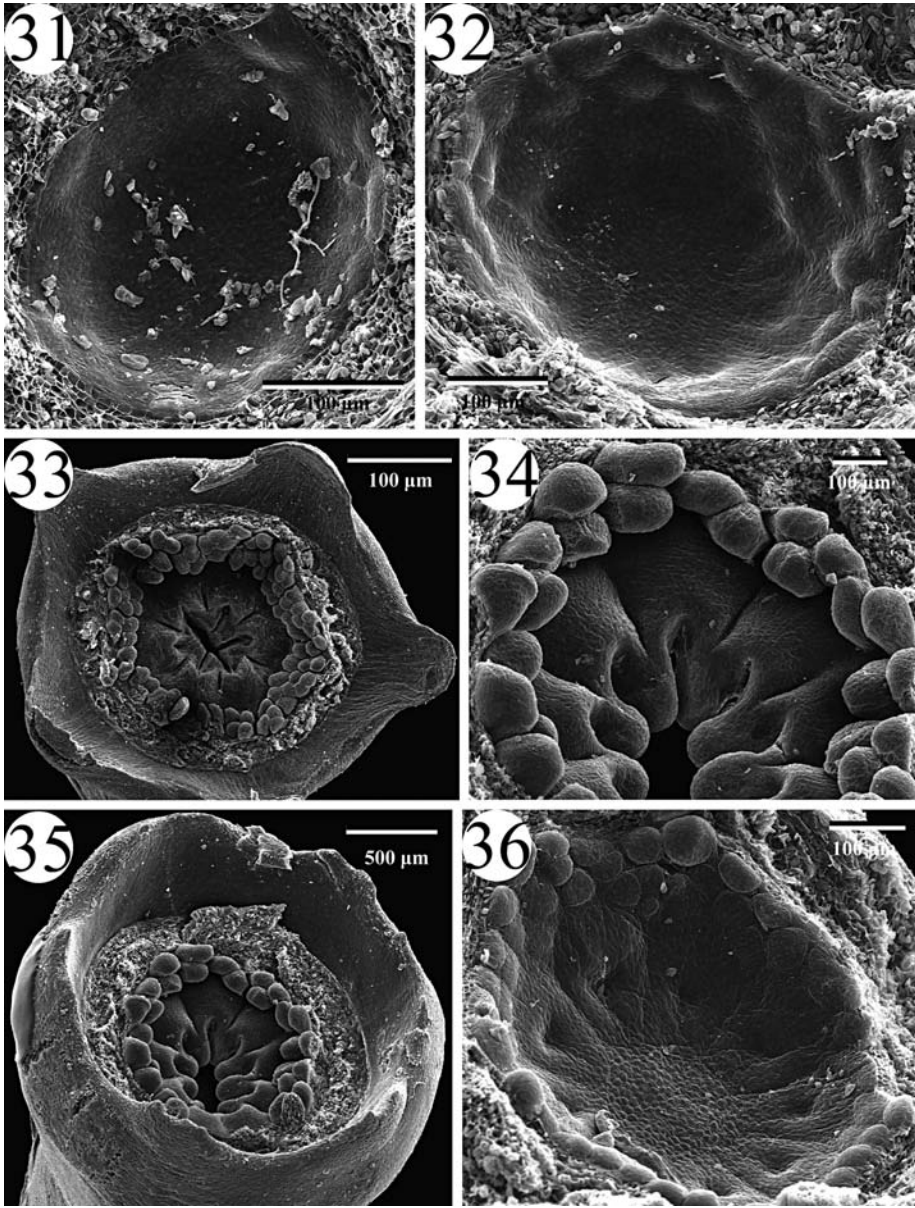


Fig. 31–36. *Plerandra* spp., a rare case of polycyclic androecium among Apiales. — 31, *P. victoriae*, the very beginning of androecium development; note the concave floral apex. — 32, *P. victoriae*, stamen initiation. — 33, *P. victoriae*, young flower, corolla removed. — 34, *P. grandiflora*, androecium and gynoecium development. — 35, *P. grandiflora*, young flower, corolla removed. — 36, *P. insoluta*, young androecium and gynoecium.

Plerandra. This is the only clearly documented case of a polycyclic androecium among Araliaceae. Lowry (1990) reported two whorls of stamens in *Tetraplasandra waialealae* and *T. waimeae*, but his data are not confirmed by our results at least for the former species. Lowry did not examine, however, the early developmental stages, in which the one-whorled condition was especially clear in our material. More data are needed (especially for *T. waimeae*) to clarify the occurrence of a two-whorled androecium in *Tetraplasandra*.

As outlined above, a regular alternation of the members of adjacent stamen whorls is not always obvious in *Plerandra*. Therefore, one might speculate that stamen arrangement is chaotic rather than whorled in *Plerandra*. Though only limited material of *Plerandra* was available for our study, we believe that the stamens generally follow arrangement in several tiers and the arrangement can be called whorled. The irregularities in alternation of the adjacent whorl members may be due to increased merism, which often leads to partial isomery (see below). An important observation made in our study is the absence of any traces of the common stamen primordia or a ring primordium in *Plerandra*. Floral vascular anatomy (Philipson 1970) shows absence of stamen trunk bundles in *Plerandra*.

The presence of more than one stamen whorl is an extremely rare condition for euasterids. Apart from *Plerandra*, it is reported from *Dialypetalanthus* (Piesschaert et al. 1997), which is now placed in Rubiaceae (Piesschaert et al. 1997, Fay et al. 2000, APG II 2003). However, stamen initiation was not documented so far in *Dialypetalanthus*, and the conclusion on presence of two whorls is inferred from observations of mature flowers only. Another possible euasterid member with several whorls of stamens is *Hoplostigma*. This genus was unplaced because of lack of the robust molecular phylogenetic data (see APG II 2003), but its position in or near Boraginaceae is most likely (e.g., Takhtajan 1997), and new molecular data support this conclusion (Stevens 2009; M.W. Chase, pers. comm.). Although the multistaminate androecium of *Hoplostigma* is described as polycyclic (e.g., Goldberg 1986), this state is not clear enough from the published illustrations, and developmental data are apparently absent.

Though a polycyclic androecium is very rare among euasterids, it occurs in some members of the two basal asterid orders, viz. Ericales and Cornales. Polycyclic polystemony is documented in Hydrangeaceae and Loasaceae (Cornales) and in 10 of 23 families of Ericales (e.g. Hufford 1998, Endress 2002, Schönenberger & Grenhagen 2005).

Another feature of *Plerandra* that is unusual for euasterids is stamen formation on a markedly concave receptacle. This condition, however, could be correlated with polycycly of the androecium, because invagination of the receptacle provides the space necessary to arrange multiple stamen whorls. Multiple stamen whorls initiating on the concave receptacle in the basipetal (i.e., morphologically centripetal) sequence is known in many groups of rosids (e.g., Leins 1964, Ronse De Craene & Smets 1991, Ronse De Craene 1992). The same pattern of polyandry is also found in some basal asterids. For example, *Plerandra* strongly resembles *Deinanthe* (Hydrangeaceae: Cornales) in its mode of androecium initiation (Hufford 1998). Moreover, stamens of adjacent whorls in *Deinanthe* sometimes lie on the same radii (Hufford 1998, Fig. 23), as we observed in *Plerandra*.

2. Meristic variation.

(A) Isomery. Isomerous (i.e., those with equal number of sepals, petals, stamens and carpels) flowers are very common in Araliaceae. Among isomerous flowers, pentamery is most common. Pentamerous flowers appear to be primitive within Araliaceae. However, members of many basal lineages (Fig. 37) have bicarpellate gynoecium in otherwise pentamerous flowers (B1, see below), and this condition could be more archaic than isomerous pentamery.

Although pentamery is common, other types of isomerous flowers occur in Araliaceae. Tetramerous flowers (along with pentamerous ones) occasionally occur in some species of *Oreopanax*, *Gamblea*, *Schefflera* (*S. venulosa*) and *Meryta* (Smith 1985). Flowers with increased merism are fairly common. For example, hexamerous flowers occasionally occur in some *Schefflera* species with normally pentamerous flowers (e.g. *S. venulosa*). The number of floral parts in isomerous whorls can reach 11–12 in *Trevesia*, *Reynoldsia* (Eyde & Tseng 1971) and some *Schefflera* species (e.g. *S. actinophylla*). Several genera show extremely polymerous flowers, e.g. *Tupidanthus calyptratus* (50–200-mery), *Scheffleropsis* spp. (up to 30-mery), *Osmoxylon* spp. (up to 30-mery). However, we should note that the flower of *Tupidanthus calyptratus* cannot be viewed as clearly isomerous because of the uncertainty regarding the merism of the corolla and the calyx in this species. For the same reason, we cannot define whether or not this flower is polystemonous, because the polyandry is the condition where the number of stamens exceeds the number of all perianth organs (e.g., Hufford 1998, Endress 2003). The uncertainty regarding the merism of the perianth in *Tupidanthus* is not due to the lack of appropriate data. Sokoloff et al. (2007) and Nuraliev et al. (2009) studied flower initiation and vascular anatomy of *Tupidanthus* in detail, but these data do not allow counting their petals and sepals. A detailed comparison of corolla vasculature in *Tupidanthus* and in related *Schefflera* species did not allow establishing homologies between them (Nuraliev et al. 2009).

Loss of isomery often occurs in polymerous flowers due to unstable organ number in all whorls (e.g. *Tupidanthus* — with respect to stamens and carpels, *Schefflera actinophylla*). In these flowers, the number of elements is not strictly the same but nearly equal in different whorls; in other words, the difference between whorls is much less than merism of each whorl. This state can be described as partial isomery.

(B) The flower is not isomerous due to carpel number only.

(B1) Oligomerous gynoecium. The gynoecium of two (sometimes three) carpels associated with pentamerous corolla and androecium is the common within Araliaceae and occurs in several lineages of this family such as *Astrotricha*, *Polyscias*, *Brassaiaopsis*, *Eleutherococcus*, etc. Although tetramery of corolla and androecium is a typical condition for *Tetrapanax*, its flower has two carpels and hence it is not isomerous (Eyde & Tseng 1971).

Molecular data (see also Fig. 37) suggest that the bicarpellate gynoecium is an ancestral condition in core Araliaceae (Plunkett et al. 1996, 1997, 2004b), but considerable infrafamilial and even infrageneric variability of carpel number makes this idea questionable (Wen et al. 2001).

(B2) Polymerous gynoecium. Increase of carpel number relative to the merism of other whorls occurs in several unrelated clades of Araliaceae (Fig. 37), for example, in

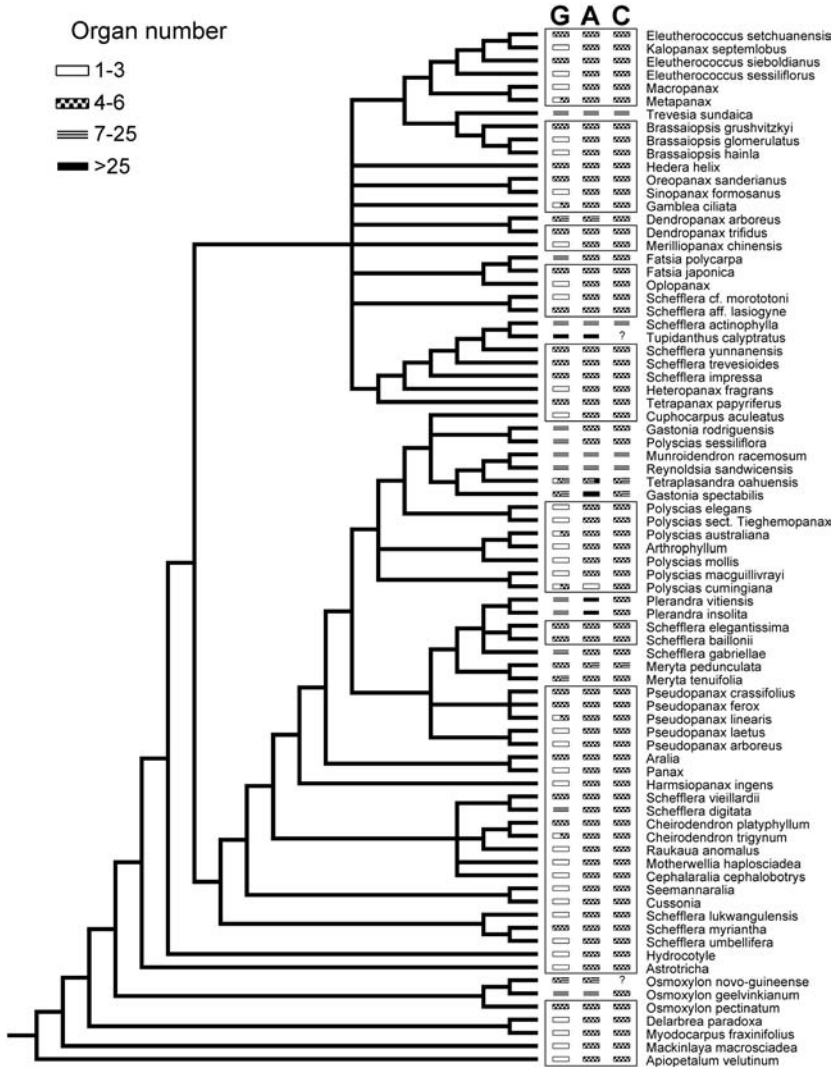


Fig. 37. Mapping of flower merism on the simplified phylogenetic tree based on Bayesian inference analysis of the combined (ITS and *trnL-trnF*) data for Araliaceae (Plunkett et al. 2004b). G=gynoecium, A=androecium, C=corolla. Large boxes show taxa where flower groundplan is typical for euasterds, i.e. corolla and androecium are 4–5(6)-merous and gynoecium is (1)2–5(6)-merous. Information on floral merism was taken from Bamps (1974), Bean (1997), Eyde & Tseng (1971), Jebb (1998), Harms (1898), Lowry (1990), Marais (1984), Philipson (1965, 1995), Reyneke (1981), Shang & Lowry (2007), Smith & Stone (1968), Smith (1985), Sosa (1979), Tennant (1968), Viguier (1910–1913), and personal observations.

Fatsia polycarpa, *Schefflera gabiellae*. Note the species *Schefflera octophylla* with the same phenomenon is not included in the figure 37 because of its absence from the phylogenetic tree used for the figure.

(C) The flower is not isomerous due to polymery of its single-whorled androecium. This condition occurs in some species of closely related genera *Tetraplasandra* and *Gastonia* (Philipson 1979), for example in *Gastonia spectabilis* (Fig. 37) and in *Tetraplasandra waialealae* studied here (not on Fig. 37). The combination of polymerous androecium with oligomerous gynoecium and corolla was regarded by Cronquist (1981, 1988) as one of the possible ancestral conditions for Araliaceae. Interestingly, the carpels of *Tetraplasandra* (at least *T. waialealae*) often alternate with petals or the orientation of these two whorls is not correlated, whereas in isomerous flowers of other Araliaceae petals and carpels lie on the same radii. A polymerous androecium is a rare feature for euasterids, but occurs quite often in basal asterids. For instance, *Carpenteria* (Hydrangeaceae, Cornales) possesses extremely specific polyandrous flowers. The androecium of *Carpenteria* develops as single-whorled but looks like consisting of several whorls in mature flowers (Hufford 1998).

Among euasterids, an interesting case of co-occurrence of isomerous and non-isomerous flowers due to the meristic variations of androecium is reported for *Theligonum cynocrambe* (Rutishauser et al. 1998). This member of Rubiaceae is characterized by unisexual flowers. Its male flowers bear only two or three perianth parts but their stamen number varies considerably within inflorescence depending on a flower position in floral cluster. Some of male flowers are isomerous, with only two or three stamens in alternipetalous position which are initiated as individual primordia. In non-isomerous male flowers, however, more numerous (up to 19) stamens are arranged into a single whorl. In such flowers, the androecium is initiated as a continuous rim dividing further into individual stamen primordia. In mature flowers some stamens of a whorl become occasionally displaced to the centre or periphery giving impression of several stamen whorls (Rutishauser et al., 1998).

Increasing stamen number in *Tetraplasandra* flowers could occur by at least two different ways: (1) by increasing merism of the androecium, i.e., by a simple multiplication of stamen primordia within stamen whorl and (2) by stamen multiplication from antesealous sectors which results in development of a fascicle of stamens instead of a single stamen from each androecium primordium. The last case can be found in polyandrous flowers of some eudicots (e.g. Ronse De Craene & Smets 1991). The presence or absence of stamen groups should be verified by investigations of early flower development (development of several stamens from antesealous common primordia) and flower vascular anatomy (presence of stamen trunk bundles). Although we had only very limited material for stages younger than illustrated in Fig. 25, our preliminary data suggest absence of common stamen primordia in *Tetraplasandra*.

3. Congenital petal fusion (*Tupidanthus calyptratus*, *Osmoxylon* spp.). Presence of the corolla tube is a key feature of the asterid clade, but in *Tupidanthus* the sympetalous corolla is transformed into a calyptra and is very distinctive from the typical asterid corolla tube in terms of its shape and function (see Sokoloff et al. 2007).

4. Variation of flower shape. The flower of *Schefflera actinophylla* changes its shape during the development from strongly polysymmetric to slightly disymmetric, in other

words, the flowers are disymmetric with early polysymmetry (*sensu* Endress 1999). At the same time, the orientation of the symmetry plane here does not depend from the position of structures surrounding the flower, such as the flower subtending bract and the bracteoles. On the other hand, in mature flowers, symmetry plane of carpel and petal arrangement finely correspond to each other and to the symmetry plane of the entire flower. This combination of features means that the formation of disymmetry is seemingly triggered by minor differences in growth rates of different sectors of a flower. It is unclear whether these differences in growth rates are due to space available in the entire growing inflorescence with closely spaced flowers.

The complicate receptacle shape in *Tupidanthus* allows insertion of a huge number of stamens and carpels in a single whorl each and facilitates compitum formation (Sokoloff et al. 2007). In some other taxa with less polymerous gynoecium (*Osmoxylon*, *Munroidendron*, some *Schefflera* species), carpel margins in symplicate zone tend to be postgenitally united in the center of the flower along a line rather than just in a central point (see also Endress 2006). This resembles the condition in *Tupidanthus*, though in a less pronounced form. However, our observations on *Schefflera actinophylla*, which is phylogenetically relatively close to *Tupidanthus*, show that its receptacle is circular and the overall flower shape remains circular until the development of the symplicate gynoecium zone. Therefore, the flower receptacle provides enough space for initiation of numerous organs (12 in each whorl), and the spatial difficulty appears only at the stage of organ joining (carpels to form a compitum and petals to protect the floral bud). This condition might be regarded as a logical step (but not necessarily a real intermediate form!) toward the *Tupidanthus* gynoecium where the symmetry is determined at early developmental stages (the flower is disymmetric or sometimes asymmetric *sensu* Endress, 1999). There is no doubt that the flower shape is strongly connected with flower merism and non-polysymmetric flowers are derived from polysymmetric. Therefore, disymmetric flower of *Tupidanthus* most likely evolved by disruption of flower polysymmetry of its ancestor. This is an argument for secondary origin of polymerous flowers.

Unusual floral symmetry in *Schefflera actinophylla* and *Tupidanthus* is to compare with that of disymmetric or even asymmetric mature flowers in *Euptelea* (Eupteleaceae: Ranunculales) (Ren et al. 2007). Unlike *Tupidanthus*, however, the flower of *Euptelea* is wider in a transverse plane than in a median plane, thus its symmetry is determined by external reasons, namely by pressure of the bract. *Euptelea* is also distinctive in non-simultaneous development of stamens as well as carpels, which causes so-called early flower asymmetry in this species. To summarize, we can mark out several reasons for changing flower symmetry such as external pressure and unevenness of androecium and gynoecium development (*Euptelea*), connection of organs in the centre of flower, including development of the compitum (*Schefflera actinophylla* and *Tupidanthus*), and arrangement of multiple organ primordia in one whorl at the limited size of flower meristem (*Tupidanthus*).

Among euasterids, bisymmetric flowers with increased stamen number are reported also from *Theligonum cynocrambe* (Rubiaceae), where numerous stamens can form an elliptic whorl (Rutishauser et al. 1998), which slightly reminiscent the androecium structure of *Tupidanthus*.

Floral polymery as a derived feature in Araliaceae

It is most likely that the polymery of flowers, which was often considered to be primitive for angiosperms in general and for Araliaceae in particular (e.g., Harms 1898, Viguier 1906, Li 1942, Takhtajan 1966, Grushvitsky & Skvortsova 1973, Grushvitsky 1981), is a derived condition within Apiales. Polymery as such, does not represent a single character state in Araliaceae. Our study revealed several different characters that should be considered separately. Several kinds of so-called “polymerous flowers” can be detected. These include (hemi)isomerous polymerous flowers, as in *Schefflera actinophylla*, flowers with (hemi)isomerous polymerous gynoecia and androecia and undefined merism of the perianth (*Tupidanthus*), flowers with one-whorled polymerous androecia and oligomerous perianth and gynoecia (*Tetraplasandra*), flowers with polymerous and many-whorled androecia and polymerous one-whorled gynoecia combined with oligomery in the perianth (*Plerandra*), and flowers with polymery confined to the gynoecia (as in *Schefflera octophylla*). These different types of “polymerous flowers” are found in different groups of Araliaceae, so they do not form a single lineage. Therefore we should agree with conclusions based on character mapping onto molecular phylogenies and propose tetracyclic pentamerous (possibly except the bicarpellate gynoecium) flower with semi-inferior ovary as ancestral for Araliaceae. Thus, we also agree with the earlier view by Cronquist (1968, 1981, 1989) based on comparative morphology. Deviations from tetracyclic occur rarely and are probably connected with deviations in flower merism. That is why we suppose these species to be derived from species with tetracyclic flowers. Similar reasoning can be applied to petal fusion. According to the discussion above we should consider taxa with highly polymerous flowers (*Tupidanthus calyptratus*, *Plerandra* spp., *Tetraplasandra* spp., *Osmoxylon* spp.) as highly derived species which originated from a pentamerous araliaceous ancestor and evolved in a very distinct way from the main evolutionary trend of euasterid flowers.

Future questions

This survey of the flower groundplan variation within Araliaceae suggests two questions that should be answered by further investigations:

1. *Why are flowers of Araliaceae so diverse and those of Umbelliferae so uniform?*

In the framework of traditional views on taxonomic placement of these families, there was a possibility to assume that Araliaceae retained a kind of primitive polymorphism, and the floral structure is more canalized in the more advanced family, Umbelliferae. Current molecular phylogenetic data are congruent with the idea of primitiveness of pentamerous flowers (possibly with dimerous gynoecium) within the Araliaceae-Umbelliferae complex (Plunkett et al. 1997, Plunkett et al. 2004a, Sokoloff et al. 2007). Traits of floral polymery appeared several times in the evolution of Araliaceae. This is clear not only from mapping cases of floral polymery onto molecular trees of the family but also from the fact that polymerous flowers of various Araliaceae are sharply different from each other in terms of their groundplan. Flowers of Umbelliferae might

be so stable because the dimery of the gynoecium is of functional significance due to the special fruit type, but this does not explain presence of a homoplastic tendency in Araliaceae.

2. *Are general regularities of spatial pattern formation in developing flowers conservative across Araliaceae and Umbelliferae?* More precisely, what is the relative impact of acropetal and basipetal patterning (*sensu* Choob & Penin (2004) and Penin et al. (2004); see also Sokoloff et al. 2008) in floral initiation in different taxa within these families? Stable orientation of the two carpels in the median plane of the flower and occasional loss of the calyx suggest an important role of basipetal patterning in Umbelliferae. Our observations on androecium and gynoecium variation in *Tupidanthus* suggest patterning of carpel sites before those of stamens (Sokoloff et al. 2007). However, such cases as the co-occurrence of sepals and petals in two regularly alternating oligomerous whorls in flowers with increased and unstable stamen number, and especially the presence of multiple carpels in otherwise pentamerous flower (e.g. *Schefflera octophylla*) can hardly be explained by the basipetal patterning model. Obviously, these data show some diversity in interplay between basipetal and acropetal patterning within Apiales that needs more detailed analysis. An important observation is variable relative position of petals and carpels in *Tetraplasandra* (i.e., some flowers are with antepetalous carpels and other are with alternipetalous carpels). This suggests independent patterning of gynoecium and perianth in *Tetraplasandra*. Certainly, flowers of Araliaceae could be an interesting subject for evo-devo investigations.

Conclusions

1. Although floral pentamery (at least in the perianth and androecium) is common within Araliaceae, almost no floral morphological features are constant. Invariable features are: whorl element arrangement, presence of a corolla, free stamens, syncarpous one-whorled gynoecium.

2. As a wide range of non-pentamerous flowers in Araliaceae suggests, deviations from the pentamerous groundplan occur independently in different groups of this family.

3. At least four major cases of evolutionary polymerization of flower occur in the family: the Asian *Schefflera* clade (incl. *Tupidanthus*), the Pacific *Schefflera* clade (incl. *Plerandra*), *Polyscias-Tetraplasandra* group, and *Osmoxylon*.

4. The following main trends of floral evolution can be distinguished: reduction of calyx, increase of stamen number and increase of carpel number with changing flower symmetry.

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