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Floral ontogeny of *Schisandra chinensis* (Schisandraceae): implications for androecial evolution within *Schisandra* and *Kadsura*

Xiao-Yu Dong · Zhong Liu · Richard M. K. Saunders · Zhi-Duan Chen

Abstract The organogenesis of staminate and carpellate flowers of *Schisandra chinensis* (Schisandraceae) was investigated with scanning electron microscopy, with observations on the development of tepals reported for the first time. The results showed that there is no interval between the initiation of the last tepal and that of the first stamen or carpel, and that the shapes of tepal, stamen, and carpel primordia are similar. The tepals and stamens of staminate flowers are initiated acropetally in a continuous spiral Fibonacci phyllotaxis, with no carpel structures observed; the filaments are not connate. The organogenesis of the carpellate flowers is similar to that of the staminate flowers, but with no evidence of stamen development. The carpels are ascidiate without postgenital fusion. Three androecial characters of *Schisandra* and *Kadsura* are discussed in a phylogenetic context. The subglobose or obovoid androecium of *Schisandra propinqua* and *Schisandra plena* may be homologous with that in sections *Kadsura* and *Sarcocarpon*. The plesiomorphic form of the androecium within the two genera is likely to be elongate with more than ten free stamens.

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Introduction

Schisandraceae sensu lato (including Illiciaceae; APG III 2009) consists of three genera: *Schisandra* and *Kadsura*, which are woody climbers with unisexual flowers and fleshy berries (Smith 1947; Saunders 1998, 2000); and *Illicium*, a genus of small to medium-sized trees with hermaphroditic flowers and dry follicles (Smith 1947). The family is classified in the near-basal order Austrobaileyales together with the Austrobaileyaceae and Trimeniaceae (Qiu et al. 1999, 2000, 2001; APG II 2003; APG III 2009) and is of considerable importance for inferring patterns of morphological evolution in early-divergent angiosperms.

Schisandra has traditionally been distinguished from *Kadsura* on the basis of differences in fruit morphology, with significant post-fertilization elongation of the receptacle in *Schisandra* (Saunders 2000) but not in *Kadsura* (Saunders 1998). However, molecular phylogenetic research has cast some doubt over the monophyletic status of the two genera (Liu et al. 2000, 2006; Hao et al. 2001; Fan et al. 2011). The most comprehensive of such studies is that of Fan et al. (2011), which was based on analysis of combined ITS nuclear ribosomal DNA sequences and sequences of five chloroplast DNA regions (*mat*K, *trn*H-*psb*A, *rbc*L, *rpl*16, and *trn*L-F). The results indicated that *S. propinqua* and *S. plena* are nested within *Kadsura* with 99% bootstrap support.

There is substantial diversity in androecial morphology within *Schisandra* (Table 1), and this has been used as one of the principal characters for subgeneric and sectional classifications (summarized by Liu et al. 2006). Saunders (2000) identified four main androecial types (designated A–D). Type A consists of 7–70 essentially free stamens on an elongated (columnar) floral receptacle, and is the most common form in the genus, occurring in species such as *S. grandiflora* and *S. sphenanthera*. These two species represent two sub-types: in the "grandiflora" sub-type theca dehiscence is extrorse to extrorse-lateral and there is no evidence of connation of distal stamens; in the "sphenanthera" sub-type, however, theca dehiscence is introrse-lateral and the distal stamens are connate. The type B androecium, observed in only three species (*S. bicolor*, *S. glabra*, and *S. repanda*), consists of a regular pentagonal shield of five horizontally oriented stamens around a broad floral apex. The type C androecium, observed in only *S. chinensis*, consists of (4–) 5 (–6) stamens on a columnar receptacle. Extensive synandry is observed in the type D androecium (in *S. propinqua* and *S. plena*), in which 4–18 stamens are fused into a carnose mass. The phylogenetic position of *S. propinqua* and *S. plena* indicated by molecular evidence (Liu et al. 2006; Fan et al. 2011) suggests that explanation of the origin of this synandry will require comparisons with *Kadsura* rather than with *Schisandra*.

The gynoecium is comparatively uniform in *Schisandra*, consisting of 12–120 carpels, spirally arranged on an elongated receptacle (Saunders 2000). Intercarpellary spaces are filled with a mucilaginous secretion that possibly acts as an extragynoecial compitum, as observed in other species in the family (Williams et al. 1993; Igersheim and Endress 1997; Lyew et al. 2007).

Information on floral ontogeny is important for understanding patterns of morphological character evolution. The morphogenesis of *Schisandra glabra* and *S. sphenanthera* flowers has been examined by scanning electron microscopy (SEM) (Tucker and Bourland 1994; Liu and Lu 1999), and several other studies also refer to organogenesis of floral primordia in *S. chinensis*, *S. rubriflora*, *S. glaucescens*, *S. propinqua* var. *sinensis*, *Kadsura japonica*, and *S. plena* (Igersheim and Endress 1997; Liu and Lu 1999; Endress 2001; Liu et al. 2001). For *S. chinensis*, most developmental stages of the androecium and gynoecium have been described (Endress 2001; Liu et al. 2001), but the development of tepals, the receptacle apex, and ovules has never been reported. Because *S. chinensis* is the sole representative of the *Schisandra* section (or subgenus) *Maximowiczia*, and the only species with the type C

Table 1 Androecial types and characteristics in *Schisandra* and *Kadsura* (Smith 1947; Law 1996; Saunders 1998, 2000; Liu and Lu 1999; Endress 2001; Liu et al. 2001, 2006)

Types		Shape of floral apex when first stamen initiated	Shape of androecium after initiation of all stamens	Degree of synandry	Number of stamens
Sensu Smith (1947) and Saunders (1998, 2000)	Sensu Law (1996), Saunders (1998, 2000) and Liu et al. (2006)				
Type A	Grandiflora type	Subglobose	Elongate or slightly elongate	Stamens essentially free	22–70
	Sphenanthera type	Slightly convex			7–35 (–40)
Type B	Glabra type	Slightly convex	Pentagonal	High degree of synandry	5
Type C	Chinensis type	Slightly convex	Elongate	Stamens essentially free	(4–) 5 (–6)
Type D	Propinqua type		Subglobose	High degree of synandry	4–18
	Plena type		Subglobose or elongate	High degree of synandry	About 8
Type E	Coccinea type		Elongate or slightly elongate	Stamens essentially free	20–70 (with up to 22 sterile appendages)
Type F	Longipedunculata type	Subglobose	Subglobose or obovoid	Stamens basally adnate with receptacle, free distally	24–74
Type G	Scandens type		Subglobose or obovoid	Stamens basally adnate with receptacle, free distally	15–57

androecium, investigation into its floral ontogeny, including all of the developmental stages, is of particular importance for interpretation of floral character evolution of the Schisandraceae. *Schisandra chinensis* is a woody liana from moist habitats in north-eastern China, Korea, far-eastern Russia, and northern Japan (Saunders 2000), and is notable for its labile sexuality, with individual plants variably bearing carpellate, staminate or both sexes of flowers, with changes observed between flowering seasons (Ueda 1988). Although individual flowers are almost always unisexual, occasional hermaphroditic flowers have been observed (Ueda 1988; Endress 2001; R.M.K. Saunders, personal observation).

The objectives of this study were:

1. to provide details of all developmental stages of staminate and carpellate flowers of *S. chinensis*, particularly emphasizing tepal initiation and its developmental sequence with stamens or carpels; and
2. to understand the variation and evolution of floral characters in the context of the most recent phylogenies of both *Schisandra* and *Kadsura*. Androecial development is of particular interest given the great variability in the genus and its distinctive form in this species.

Materials and methods

Floral anatomy

Young buds at different developmental stages were collected in May of 2006, 2007, and 2008 from Dongling Mountain and Wuling Mountain near Beijing, and Tonghua, Jilin Province, respectively. The buds were either vegetative (containing leaf primordia) or mixed (with both leaf and floral primordia), but the two types could only be distinguished after dissection. Voucher specimens (*Fan20060514-01*; *LD20080523-12*) have been deposited in the Herbarium, Institute of Botany, Chinese Academy of Sciences, Beijing (PE).

The material was fixed in FAA (5:6:89 mixture of formaldehyde, glacial acetic acid, and 50% ethanol) for more than 24 h and then transferred to 70% ethanol for storage. The buds were dissected in 95% ethanol under a stereomicroscope. After dissection, the buds were further dehydrated through a graded series of ethanol–isoamyl acetate, and dried in a Hitachi HCP-2 critical-point drier with liquid carbon dioxide for 1 h. The buds were then attached to aluminum stubs, sputter-coated with gold palladium for 100–130 s using a Hitachi E-1010 sputter coater at 15 mA, and examined under a Hitachi S-4800 scanning electron microscope (SEM) at 10.0 kV.

Androecial character analysis

Parsimony methods were used to infer evolutionary transitions in androecial characters, using Mesquite version 2.6 (http://mesquiteproject.org). Three characters, androecial shape, degree of synandry, and number of stamens, were optimized on a modified strict consensus tree derived from Fan et al. (2011). Character states were scored using data from existing monographs (Smith 1947; Saunders 1998, 2000). Saunders (2000) suggested that the androecium of *S. plena* is more or less elongate, whereas Smith (1947) and Law (1996) considered it subglobose or obovoid; Liu et al. (2001) supported the latter interpretation, following studies of floral organogenesis. We have followed Liu et al. (2001) in coding the androecium of *S. plena* as subglobose/obovoid.

Results

Organography

The inflorescences of *S. chinensis* are axillary, consisting of 3–5 flowers (staminate, carpellate, or a combination of both: Fig. 1a). The staminate flowers usually contain five stamens, which are white and clearly visible (Fig. 1b). Each carpellate flower has 20–35 pale green carpels, which are free and spirally arranged on the receptacle (Fig. 1c). The size, number, colour, and shape of the tepals are similar in both staminate and carpellate flowers. Each flower has 6–9 (–10) oblong tepals (Fig. 1a–c): the two outermost tepals are pale yellow and coriaceous, with marginal cilia; the innermost 3–4 tepals are cream-coloured (pink towards the base) and membranous; and the tepals in the middle zone are transitional in both colour and texture.

Floral primordia and tepal organogenesis

The leaves develop acropetally within young inflorescences (Fig. 2a), with floral primordia developing in the axil of a young leaf (Fig. 2b, c). The innermost flowers are initiated when the organs in the outermost young flower have become more fully differentiated (Fig. 2b). Mixed buds (containing both leaf and floral primordia) consist of flowers of either only one gender (Fig. 2b) or both genders (Fig. 2c).

The floral primordium (Fig. 2d) is initially hemispherical but gradually elongates laterally, with one side enlarging as the first tepal is initiated (Fig. 2e). The second tepal primordium is initiated at a divergence angle of almost 180° to the first tepal primordium (Fig. 2f), but this angle tends towards 137.5° as subsequent tepals develop.
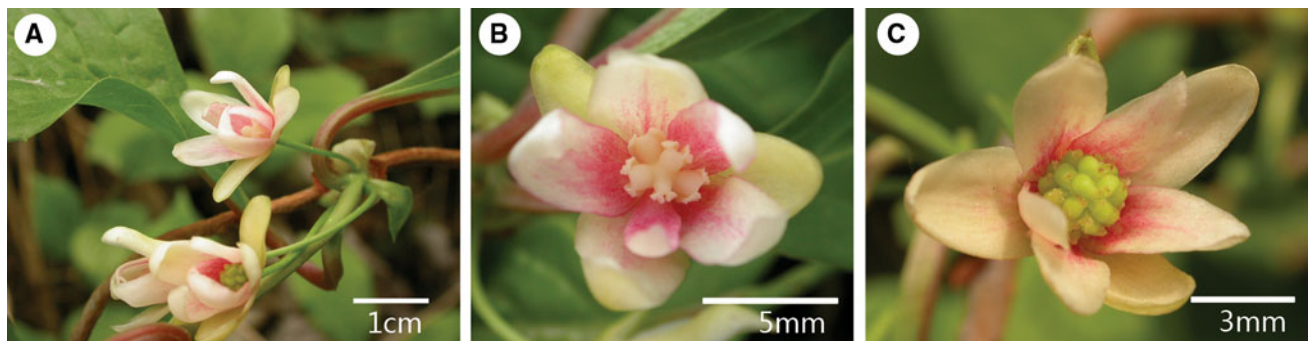
Fig. 1 *Schisandra chinensis*. Staminate and carpellate flowers. **a** Flowers of both genders in a single inflorescence (upper flower staminate, lower flower carpellate); **b** staminate flower with five *white* stamens; **c** carpellate flower with *pale green* carpels

The young flower continues to enlarge and other tepal primordia are initiated acropetally in a continuous spiral phyllotaxis, with the angles of divergence of two successive tepals approaching 137.5° (Fig. 2i). All tepal primordia are hemispherical at first, then enlarge laterally and become slightly curved as they grow (Fig. 2g). The first and second tepals initially completely cover the remaining floral apex (Fig. 2h), but as the centre of the young flower expands, the floral apex (indicated by an asterisk in Fig. 2i) can be seen without removing the tepals. The upper halves of the two outermost tepal primordia have irregular margins that develop a fringe before completing differentiation (Fig. 2j, k). The outermost two or three tepals enlarge, covering the inner organs again when all organs are initiated (Fig. 2l, m). The pattern of tepal development is similar in both staminate and carpellate flowers.

Androecial development

The interval between the initiation of the last tepal and the first stamen is equivalent to that between the initiation of two tepals. The stamens are initiated acropetally, and the divergence angles of the last tepal primordium and the first stamen primordium and that of successive stamens are all approximately 137.5° (Fig. 3a–c). Because of the regularity of the divergence angle and the morphological similarity between the young tepals and stamens, it is difficult to distinguish between the two organs before the formation of the pollen sacs (Fig. 3a). The young stamens gradually appear cuboidal in polar view (Fig. 3b, c), with the four corners expanding rapidly and developing into pollen sacs (Fig. 3d). The stamens elongate, and, because the adaxial face of the connective tissue develops more rapidly than the abaxial face, the two thecae become extrorse at maturity (Fig. 3e, f). The centre of the whole flower continues to elongate throughout organogenesis, ultimately forming a columnar receptacle. At no stage is there any evidence of carpel initiation or abortion.

Gynoecial development

As with the transition from tepals to stamens in the staminate flowers described above, the interval between the initiation of the last tepal and the first carpel in carpellate flowers is equivalent to that between the initiation of two subsequent tepals. The divergence angle between the last tepal primordium and all subsequent carpel primordia is consistently approximately 137.5° (Fig. 4a–e). The carpel primordia are uniformly hemispherical, but are noticeably smaller than the tepal and stamen primordia; this size difference can therefore be used to distinguish the two genders of flowers at an early stage (Fig. 4a). As the gynoecium matures, the carpels become ovoid with terminal expansion to form a bilobed stigma (Fig. 4e, f) that lacks a true style.

During the development of individual carpels, growth of the basal and apical part is not evident when the young carpel begins to curve toward the ventral side (Fig. 4g); the apical part subsequently grows (circled in Fig. 4h) followed by the lower region, which forms the locule (Fig. 4i). The terminal mouth of the locule forms a cleft as the carpel matures, with secretions on and around it (Fig. 4f, j). As the carpel grows, adaxial deformation results in the ascidiate part (Fig. 4h, i). In mature carpels, the distance from the lower point of the cleft to the connection of the carpel to the receptacle is approximately 500 μm, reflecting conspicuous growth of the lower part of the carpel (Fig. 4j, l). Each carpel contains two ovules (Fig. 4m).

Evolutionary transitions in androecial morphology

The results of the analyses of androecial morphological character evolution are shown in Fig. 5. The pentagonal and subglobose/obovoid androecial shapes each arose once (Fig. 5A), with evidence for the homology of the subglobose/obovoid androecia of types F, G, and D. The
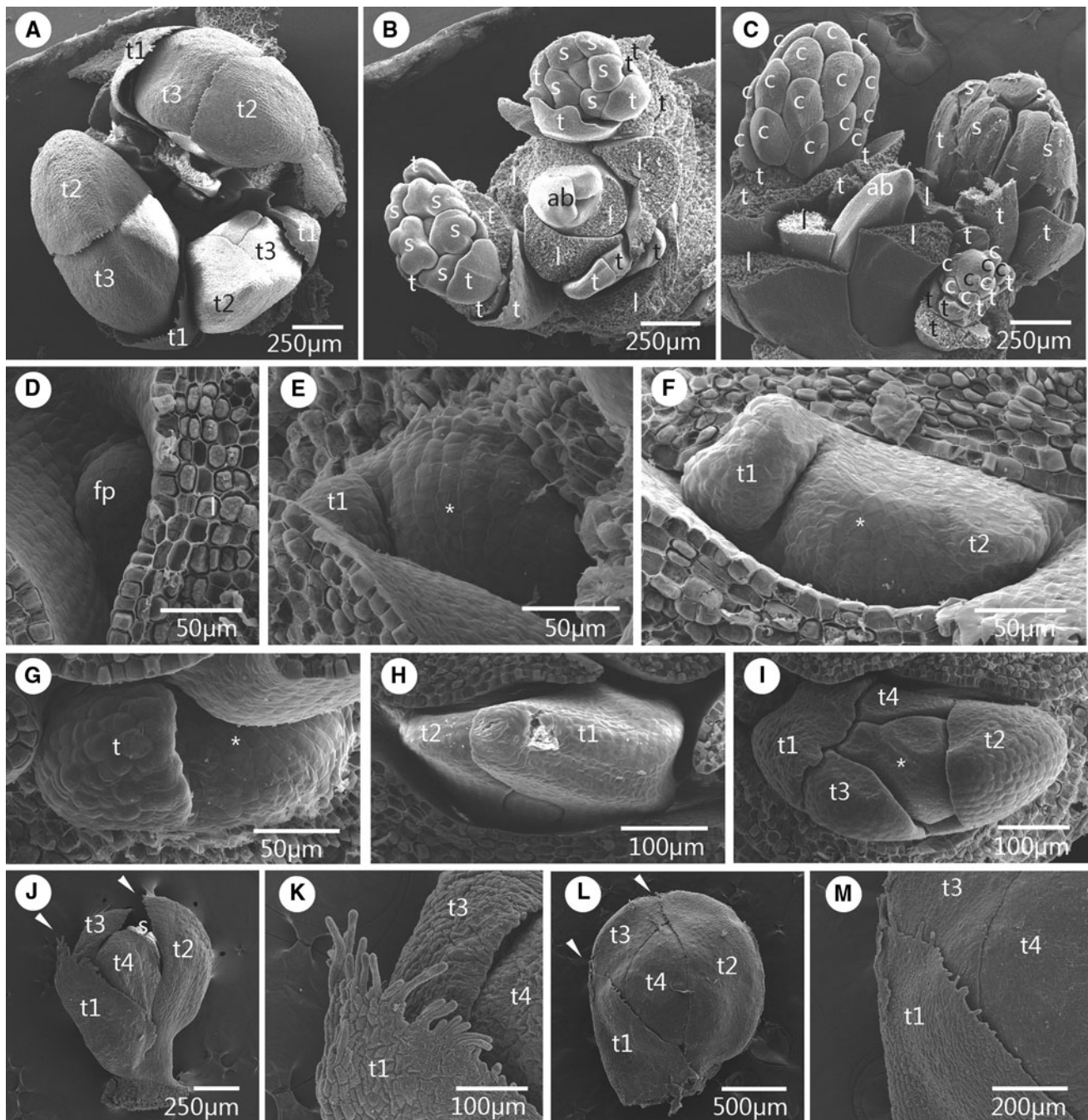
Fig. 2 *Schisandra chinensis*. Young flowers and tepal development (**a–c** young flowering shoots; **d–m** organogenesis of individual flowers). **a** Three flowers with tepals in place, **b** two staminate flowers with tepals partially removed and one inner flower at an early developmental stage, **c** a mixed shoot with two carpellate flowers and one staminate flower, **d** a floral primordium in the axil of a leaf, **e** a young flower extending laterally because of the formation of the first tepal, **f** a young flower showing continued development of the first tepal, and with a second tepal initiated on the opposite side, **g** a flower with a tepal that is beginning to curve, **h** a flower with its outermost two tepals covering the centre, **i** a flower with four tepals initiated and its centre expanded, **j** a flower with almost fully developed tepals; *arrows* indicate fringes on the margins of the two outermost tepals, **k** magnification of margin of tepal shown in Fig. 2j, **l** a flower with all tepals formed; *arrows* indicate fringe on the margin of the outermost tepal, **m** magnification of the margin of the tepal shown in Fig. 2l. *ab* apical bud of inflorescence shoot, *c* carpel, *fp* floral primordium, *l* leaf, *s* stamen, *t* tepal; *asterisk* centre of the remaining floral primordium. *Numbers* indicate the order of initiation of the organs

plesiomorphic state of the androecial shapes in clades I and II and the combined *Schisandra–Kadsura* clade is elongate/ slightly elongate, but the plesiomorphic state for the

Schisandraceae as a whole (including *Illicium*) is equivocal. Synandry arose twice, corresponding to types B and D (Fig. 5B). The plesiomorphic androecium with free

stamens is shown in clade I and clade II, and in the combined *Schisandra–Kadsura* clade. Reduction in the number of stamens arose at least twice, once in type D and again in clade I (Fig. 5C). Androecia consisting of more than ten stamens is plesiomorphic for *Schisandra* and *Kadsura*, but the ancestral condition is equivocal for clade I.

Discussion

Tepal development

In this study, we add new data on the development of tepals in both staminate and carpellate flowers of *S. chinensis* (Schisandraceae). Tepal phyllotaxis is acropetal and follows a Fibonacci pattern: the initiation corresponds with the most common pattern in spiral flowers (Endress 2008), in which the initial two tepal primordia are transverse, with subsequent organs approximating a Fibonacci spiral (Fig. 2f, i). As noted by Endress (2008), the outermost tepals seem to protect the floral apex during early development (Fig. 2h); the outer tepals subsequently do not grow significantly and the protective function is taken over by the inner tepals as the flowers grow. In our study, however, the second tepal still covers most of the flower

Fig. 4 *Schisandra chinensis*. Gynoecium and carpel development ▶ (**a–f** carpellate flower development; **g–l** development of individual ascidiate carpels). **a** Young flower with carpels being initiated, **b** slightly older flower with development of outer carpels, **c** gynoecium from the side, with entire complement of carpels initiated; changes in the shape of the carpels evident, **d** gynoecium from above, showing ovoid carpels, **e** fully differentiated gynoecium, showing the bilobed stigmas with protuberances, and absence of styles, **f** fully differentiated gynoecium with most carpels removed revealing columnar receptacle; *arrow* shows spiniform apex of the receptacle, **g** two carpels with adaxial sides beginning to curve; *arrows* show direction of curvature, **h** carpel with sides and apex curving; *arrows* show direction of curvature; *circle* shows carpel apex, **i** a carpel with sides, apex, and base of the adaxial face developing and forming a locule; *arrows* show direction of curvature, **j** adaxial face of a single carpel; *arrows* show cleft formed after sealing of locule, **k** abaxial face of a single carpel, **l** side view of a single carpel; *arrows* show cleft formed after sealing of locule, **m** side view of a single carpel, dissected to reveal ovules. *c* carpel, *o* ovule, *sc* secretion, *t* tepal. *Numbers* indicate the order of organ initiation

during the later stages of development; this might be related to the similar size of the outermost and innermost tepals. According to Endress (2008), in basalmost angiosperms with spirally arranged flowers, for example *Amborella* and Austrobaileyales, the smaller the outer tepals are, the greater the number of tepals. *Schisandra chinensis* has only 6–9 (–10) similar-sized inner and outer tepals; the protective function of the outer tepals is not completely
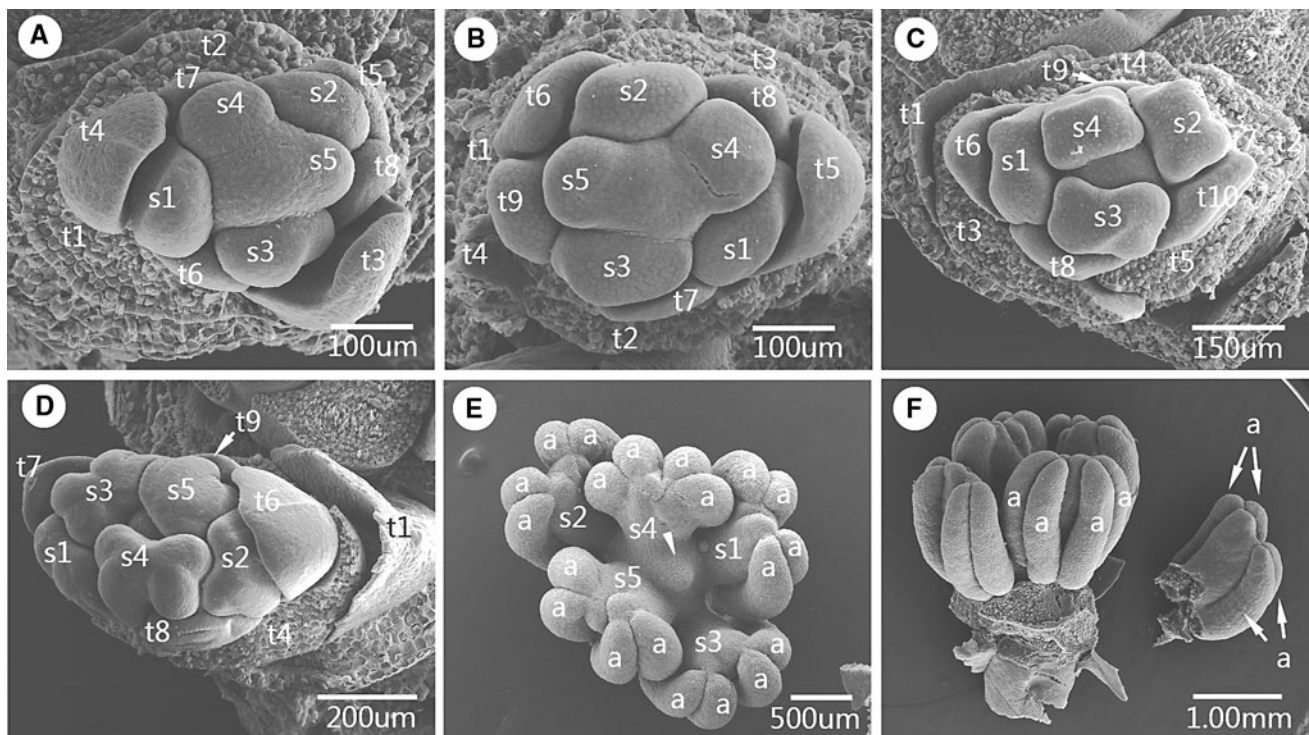

Fig. 3 *Schisandra chinensis*. Androecium development. **a** All tepals and stamens initiated, **b** slightly older flower, **c** slightly older flower with stamens 4-angled, **d** slightly older flower with pollen sacs bulging, **e** slightly older flower with extrorse anthers; centre of the flower forms a columnar receptacle; *arrow* shows a spike-like structure, **f** side view of fully differentiated androecium; one stamen removed (shown on *right* of figure). *t* tepal, *s* stamen, *a* pollen sac. *Numbers* indicate the order of organ initiation
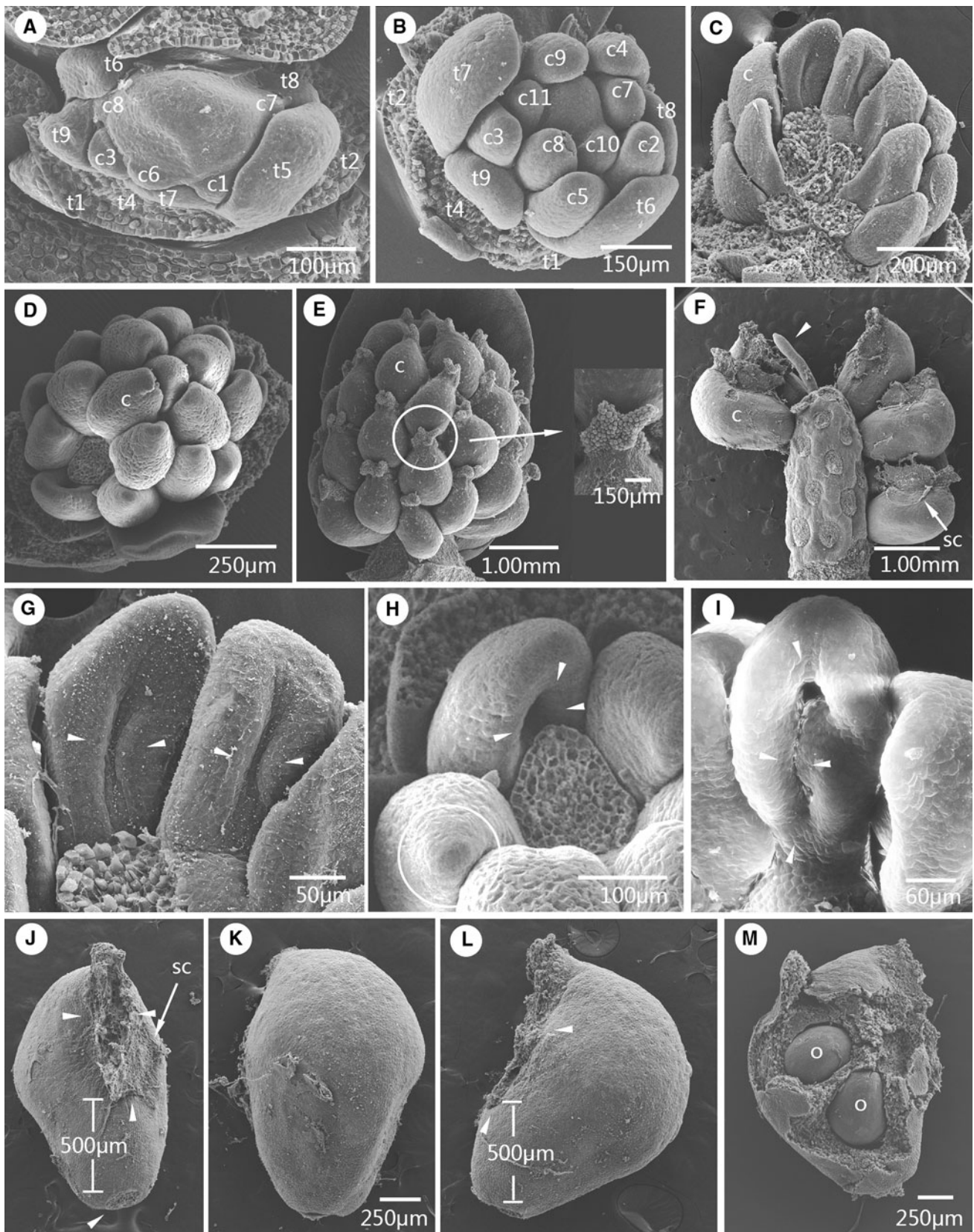
Fig. 5 Parsimony inference of evolutionary patterns of androecial characters in *Schisandra* and *Kadsura*, using Mesquite version 2.6. Phylogenetic tree is modified based on Fan et al. (2011)
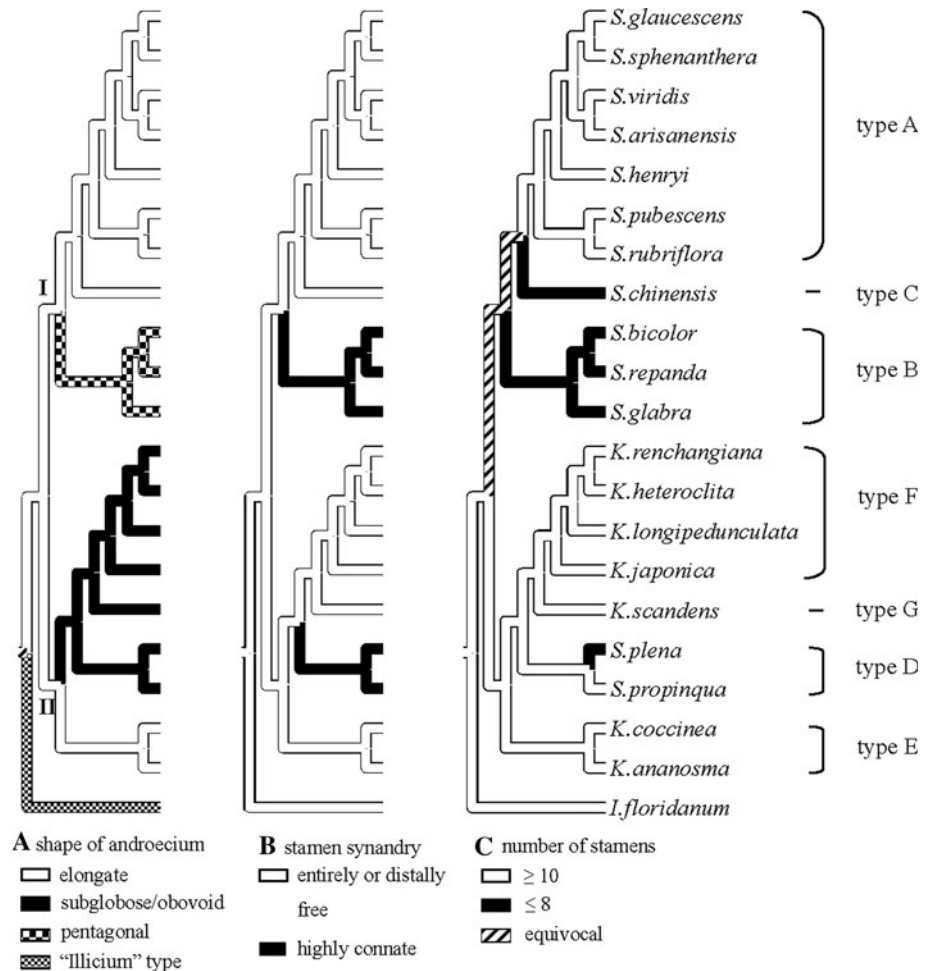
replaced by that of the inner tepals, because of the paucity of tepals.

There is no interval between the initiation of the last tepal and that of the first stamen or carpel, and the shapes of the tepal and stamen primordia are similar. It is therefore difficult to distinguish the first stamen primordium before it becomes cuboidal. The carpel primordia are smaller than the stamen primordia; this character can therefore be used to distinguish the two genders at an early stage.

Carpel formation

The carpels of *S. chinensis* are essentially ascidiate (sensu Endress 1994) although the carpel opening, which remains unfused, is directed to the inner (adaxial) surface, protected by other carpels towards the centre of the flower (Igersheim and Endress 1997; Endress and Igersheim 2000). The intercarpellary space is filled with a mucilaginous secretion, which is likely to function as an extragynoecial compitum, as has been demonstrated for other species in this family (Igersheim and Endress 1997; Endress and Igersheim 2000; Lyew et al. 2007; Endress

2010). The adaxial position of the carpel opening results from the extensive development of the abaxial side. Studies of the vascular supply of *Schisandra* carpels have shown that the ovules are supplied either by the dorsal trace alone (*S. grandiflora* and *S. neglecta*: Jalan 1966; *S. rubriflora*: Melville 1969) or by a combination of both dorsal and ventral traces (*S. sphenanthera*: Ozenda 1946, 1949; *S. glabra*: Tucker and Bourland 1994). Bailey and Swamy (1951) correlated the apparent reduction of the ventral traces in some species with this "adaxial deformation" of the carpel.

Androecium development and the floral apex appendage in *S. chinensis*

Schisandra chinensis sometimes has a spike-like structure at the apex of the receptacle in staminate flowers (indicated with an arrow in Fig. 3e), which is presumably homologous to that observed in some carpellate flowers (upper arrow in Fig. 4f). Equivalent structures have been reported in carpellate flowers of *S. sphenanthera* (Liu and Lu 1999) and *S. glabra* (Tucker and Bourland 1994), and are

generally interpreted as the result of continued growth of the apical residuum (Tucker and Bourland 1994). It is possible that this elongated floral apex may assist in protecting the carpel openings of the innermost carpels, although there are no empirical data to support this conjecture. Some studies (Saunders 2000) suggest a degree of connotation of the base of the filaments associated in part with enlargement of the receptacle in the type A androecium, but also occurring in the type C androecium. The results presented here on the ontogeny of the staminate flower of *S. chinensis* do not support such an interpretation: filaments were not observed in this study, contradicting the description published by Liu et al. (2001).

Evolution of androecial characters in *Schisandra* and *Kadsura*

Saunders (2000) identified four main androecial types (A–D) in *Schisandra*, corresponding to the four sections recognised by Smith (1947). Law (1996) recognised six subgenera in *Schisandra* based on androecial type, and this classification was adopted by Liu et al. (2006). All these researchers agree that there are three types of androecia in *Kadsura*, labelled E–G in this study (Table 1).

The reconstruction of the evolution of androecium shape suggests that the subglobose/obovoid type originated only once in *Schisandra* and *Kadsura*. Androecia of types F and G are generally regarded as similar (Smith 1947; Saunders 1998), but the homology of the subglobose/obovoid androecia of types D, F, and G has seldom been considered. Species with androecial types F and G are shown to be monophyletic, supporting Saunders' (1998) taxonomic treatment.

The Mesquite analyses demonstrate that the ancestral state of the androecium of the two genera is more or less elongate with more than ten free stamens. The combination of these characters also appears in types A and E. This result is consistent with deductions drawn by Smith (1947), although he evaluated the primitive androecial type in the two genera separately.

Spiral phyllotaxis and floral sex

Despite the extensive morphological diversity of androecia in *Schisandra* and *Kadsura*, the pattern of organogenesis is nearly identical. All floral organs are spirally arranged, although the staminate flowers of *S. glabra* have a pentagonal shield-like receptacle with stamens that are arranged in a whorl at maturity (Tucker and Bourland 1994; Liu and Lu 1999; Endress 2001, 2008; Endress and Doyle 2007; Liu et al. 2001). According to the criterion of spiral arrangement with equivalent divergence angles and equivalent plastochrons (Endress and Doyle 2007; Endress 2008), the floral ontogeny of *Schisandra* and *Kadsura*

follow a typical Fibonacci pattern, with equivalent intervals in and between all floral organs (tepals and stamens/carpels). In basalmost relictual angiosperms such as *Amborella* and Austrobaileyales, floral organs are spirally arranged; most flowers of Nymphaeales have whorled organs, but *Nuphar* has its outermost five or six organs spirally arranged (Endress 2001). The floral organ arrangement of members of the Hydatellaceae is unknown because of its extremely simplified structure (Rudall et al. 2007, 2008; Friedman 2008).

Among early relictual angiosperms, *Schisandra* and *Kadsura* flowers are strictly structurally and functionally unisexual: no rudiment of the opposite sexual organ is observed during floral organogenesis. Apparently bisexual flowers of *K. japonica* and *S. chinensis* have been found occasionally (Ueda 1988; Endress 2001; R.M.K. Saunders, personal observation), but there is no information on the fertility of the stamens and carpels. In *Schisandra* and *Kadsura* species for which ontogeny is known, floral development is very consistent in staminate and carpellate flowers, with almost identical organogenesis irrespective of androecium type (Tucker and Bourland 1994; Liu and Lu 1999; Endress 2001, 2008; Endress and Doyle 2007; Liu et al. 2001). Endress (2001) has stated that the flowers of basalmost angiosperms can easily become unisexual because of the low level of synorganization between organs. These phenomena may indicate the importance of studying the regulatory mechanism of sex determination of floral organs in these two genera. As *Schisandra* and *Kadsura* are unusual among basal angiosperms in having strictly structurally and functionally unisexual flowers, this mechanism might aid understanding of the diversity in the origin of unisexual flowers.

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