

Inflorescence and floral development in *Trochodendron aralioides* (Trochodendraceae)

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Abstract In the early development of *Trochodendron aralioides* (Trochodendraceae) inflorescences lateral flowers are initiated after the appearance of the floral pherophylls (subtending bracts). The terminal flower is preceded by metaxyphylls and is initiated earlier than the uppermost lateral flowers of the botryoid inflorescence. Small scales (interpreted as rudimentary perianth organs) precede the stamens. These scales are more distinct in the terminal flower than in the lateral flowers. In the radially symmetrical terminal flower, small scales (or metaxyphylls) and stamens are initiated in a spiral during early development. At anthesis, stamen phyllotaxis appears irregular or approximately whorled as a result of the rapid elongation and irregular slight curvature of the stamen filaments which distorts the originally regular pattern. Finally, the numerous carpels arise simultaneously in a single whorl. It takes about 9 months for flowers to develop and the 2-year reproductive cycle of *T. aralioides* is typical of many trees. The floral development of *T. aralioides* is compared with that of other basal eudicots. The bottle-shaped, unicellular stigmatic papillae and long, decurrent stigma of basally united carpels are similar to those of the Buxales, suggesting a close relationship.

Keywords Basal eudicots · Floral bracts · Floral phyllotaxis

Introduction

Trochodendron contains a single extant species, *Trochodendron aralioides*, which belongs, together with the monotypic *Tetracentron*, to Trochodendraceae (Endress 1993). Today, *Trochodendron* occurs only on islands in East Asia (Taiwan, Ryukyu Islands, Japan) (Li and Chaw 1996). However, early fossil fruit remains closely related to the Trochodendraceae have been found in the Lower Cretaceous Potomac Group, and fossil leaf remains are known from the Early Cretaceous (late Albian) (Upchurch 1984; Crane 1989) and were widely distributed in the Northern Hemisphere during the Miocene (Iljinskaya 1972; Manchester et al. 1991; Pigg et al. 2007).

In Taiwan, *T. aralioides* grows in the cloud–fog zone along the Central Mountain Range (Su 1984) and in mountainous areas of the north-eastern region that are affected by monsoons. It is an evergreen tree and has terminal shoot or inflorescence buds with papyraceous bud scales. The inflorescences contain eight to 23 bisexual flowers. Flowers of *T. aralioides* have numerous stamens and many basally fused carpels. The perianth is reduced and represented only by numerous small scales (Endress 1986). Pollen morphology and embryo development of *Trochodendron* have been studied previously (Yoffe 1962; Endress 1986; Hsu et al. 2013). There are two types of individuals in a population: protandrous and protogynous plants, which differ in the relative timing of stigma maturation and pollen grain release (Chaw 1992; Li and Chaw 1996).

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The order Trochodendrales has been considered to be a primitive order of dicots in traditional classifications and was often related to the Magnoliidae or Hamamelidae on the basis of anther morphology and the presumed absence of vessels in the wood (Smith 1945; Pervukhina and Yoffe 1962; Cronquist 1981; Endress 1986, 1989). However, Trochodendraceae are considered to form an early diverging eudicot lineage, based on recent molecular phylogenetic results (see, for example, Worberg et al. 2007). Although in the past century *Trochodendron* was considered not to have vessels, recent SEM studies showed the existence of vessel elements in both *Trochodendron* and *Tetracentron* (Li et al. 2011). Studies of mature floral structure and aspects of floral development of *Trochodendron aralioides* were published earlier (Pervukhina and Yoffe 1962; Endress 1986, 1990). However, the present study is a complete and detailed investigation of the inflorescence and flower development in *T. aralioides* using SEM. As a number of basal eudicots have recently been studied in the same way, more comparisons among the taxa are now possible.

Materials and methods

Both protandrous and protogynous flower buds of *T. aralioides* were collected from ErhKe Mountain (678 m a.s.l.), New Taipei City, Taiwan, about once a month from June 2009 to April 2010 and from June 2013 to April 2014. Dissected buds of inflorescences at different developmental stages were fixed in 1% glutaraldehyde. Floral tissues were dehydrated in an alcohol–acetone series (50% ethanol, 70% ethanol, 85% ethanol, 95% ethanol and twice in 100% ethanol), stored in 100% ethanol, critical point-dried in CO₂ and mounted on aluminium stubs. The specimens were sputter-coated with gold (Chen 1986) and then observed by SEM (FEI Quanta 200, Academia Sinica, Taipei).

Results

In northern Taiwan, inflorescences and shoots of *T. aralioides* are initiated from June to July and develop on the tips of branches on the sunny side of the trees. They are covered by green bracts during the early stages of development and the bracts turn whitish green later.

Inflorescence

Both protandrous and protogynous individuals have inflorescences with numerous bisexual flowers (Fig. 1b, c, e, f). Inflorescences are racemes, with a terminal flower

(botryoid) (see also Endress 1986) and occasional lateral branches of the second order at the base (Figs. 2, 3b). All flowers of an inflorescence start anthesis more or less simultaneously (Fig. 1a, d).

Flowers are arranged spirally on the inflorescences axis, in a set of three anticlockwise and five clockwise parastichies (Fig. 3a–e), corresponding to a Fibonacci spiral phyllotaxis. The lower lateral flowers develop earlier than the upper ones; however, the terminal flower differentiates earlier than the immediately adjacent lateral flowers (Fig. 3f, g), as is common in botryoids (Fig. 4a, d).

Bracts and perianth-like structures

Three kinds of bracts can be distinguished, based on their position on the inflorescence: pherophylls, prophylls, and metaxyphylls (Fig. 5). Each lateral flower develops in the axil of a pherophyll (= subtending bract) (Figs. 3a, b, 4d). At anthesis, the linear pherophylls are shed. In lateral flowers, two prophylls are formed almost simultaneously in the transverse position, shortly before the floral organs are initiated (Fig. 4d). At an early stage, they are tiny and semicircular (Fig. 4e). In some flowers, the prophylls are not exactly opposite at anthesis (Fig. 4l). This occurs more frequently in the lower lateral flowers of protandrous individuals. Prophylls are larger in the lower than in the upper lateral flowers (Fig. 4e, f) and vary in protandrous and protogynous individuals (Fig. 4k, l). The terminal flower is preceded by three or more spirally arranged metaxyphylls (Fig. 4a). At anthesis, these metaxyphylls are variable in shape (Fig. 4b, c).

In addition to the three bract types described above, small scales (residual perianth organs, see also Endress 1986) appear between the metaxyphylls and androecium of the terminal flower or between the prophylls and the androecium of lateral flowers. In the terminal flower, there is a continuous transition between the shape of metaxyphylls and small scales and their phyllotaxis is spiral (Fig. 4b, c). The number of small scales varies from zero to three in lateral flowers (Fig. 4e, f, k, l) and is around six to eight (including metaxyphylls) in the terminal flower (Fig. 4b, c).

The epidermal cells of all bracts show similar morphology at anthesis. The adaxial epidermal cells of pherophylls and metaxyphylls are flat (Fig. 4g, i), and the abaxial epidermal cells of the central area are papillate when the bracts are linear and >0.5 mm wide (Fig. 4h, j). When the bracts are triangular, semicircular, or <0.5 mm wide, the abaxial epidermal cells are flat.

Androecium

Lateral flowers have non-radially symmetrical receptacles and stamens initiate earlier on the abaxial than the adaxial

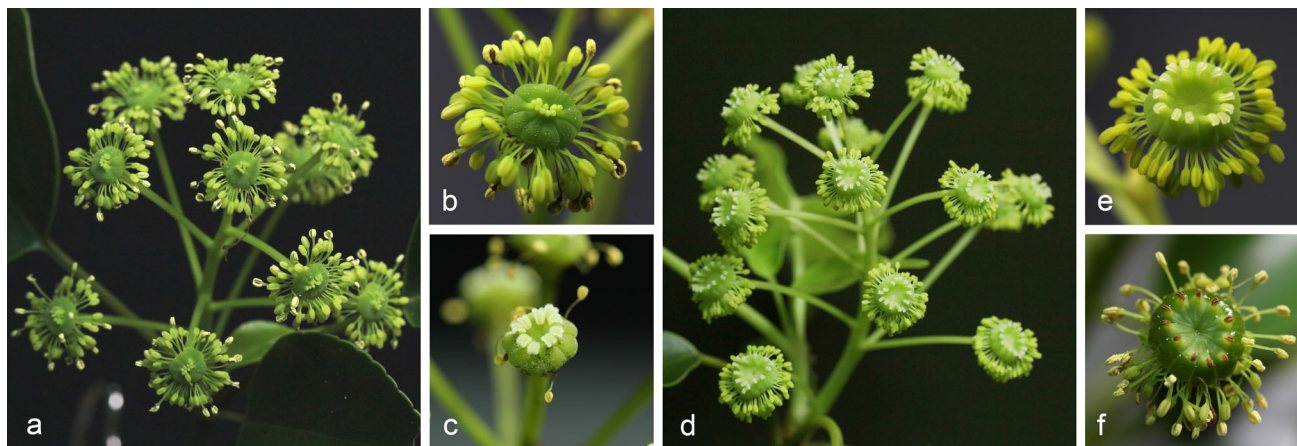


Fig. 1 *Trochodendron aralioides*. Mature flowers and inflorescences. **a** Botryoid inflorescence of a protandrous individual. **b** Protandrous flower at the mature stamen stage. **c** Protandrous flower at the mature

pistil stage. **d** Botryoid inflorescence of a protogynous individual. **e** Protogynous flower at the mature pistil stage. **f** Protogynous flower at the mature stamen stage

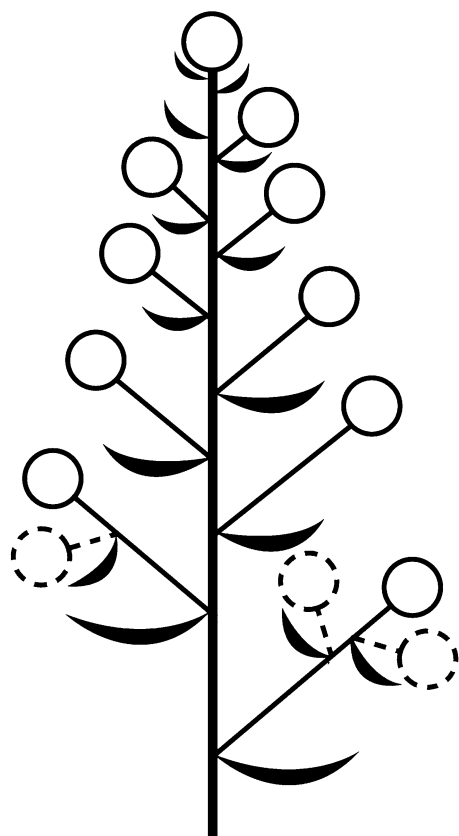


Fig. 2 *Trochodendron aralioides*. Diagram of the botryoid inflorescence

side of the floral meristem (Fig. 6a, b). The arrangement of stamens is spiral (Fig. 6c–f). There are more stamens on the abaxial side than on the adaxial side. In terminal flower, the stamens arise spirally on a flat receptacle (Fig. 7a) (see also Endress 1990). In most of the terminal flowers examined with young stamens, the most obvious numbers

of clockwise and anticlockwise parastichy sets were 13 and 8, respectively (Fig. 7b, c).

Young stamens are difficult to distinguish from developing scales (Fig. 6a, b). When they become rod-shaped (Figs. 6d, e, 8a), they differentiate into filament and anther (Fig. 8b), after which two thecae form, each with two pollen sacs (Fig. 8c, d). The filaments elongate and lift the anthers to release the mature pollen grains at the mature stamen stage (Fig. 1b, f).

Carpels

The numerous carpels arise simultaneously in a ring inside the young inner stamens (Fig. 9a). The central area of the floral apex remains flat and undifferentiated (Fig. 9a–d). The carpels become plicate and form a deep ventral slit (Fig. 9c, d). The basal edges of carpels fuse congenitally with neighbouring ones during development (Fig. 9c, d). Along the upper ventral slit, the style recurves due to excessive growth of the ventral region of each carpel before the stigmas are receptive (Fig. 9g). The stigmas have bottle-shaped unicellular papillae (Fig. 9g, h). Nectaries form on the dorsal side of the carpels (Fig. 9e, f). They secrete nectar when the anthers release pollen grains. Although the area of the floral apex remains undifferentiated, it is later covered by the carpels.

Inflorescence and flower development and phenology

The development of inflorescences and flowers in *Trochodendron* can be divided into four stages (Table 1): inflorescence primordium formation (stage 1), floral primordium formation (stage 2), floral organ development (stage 3) and anthesis (stage 4). In Taiwan, the formation of

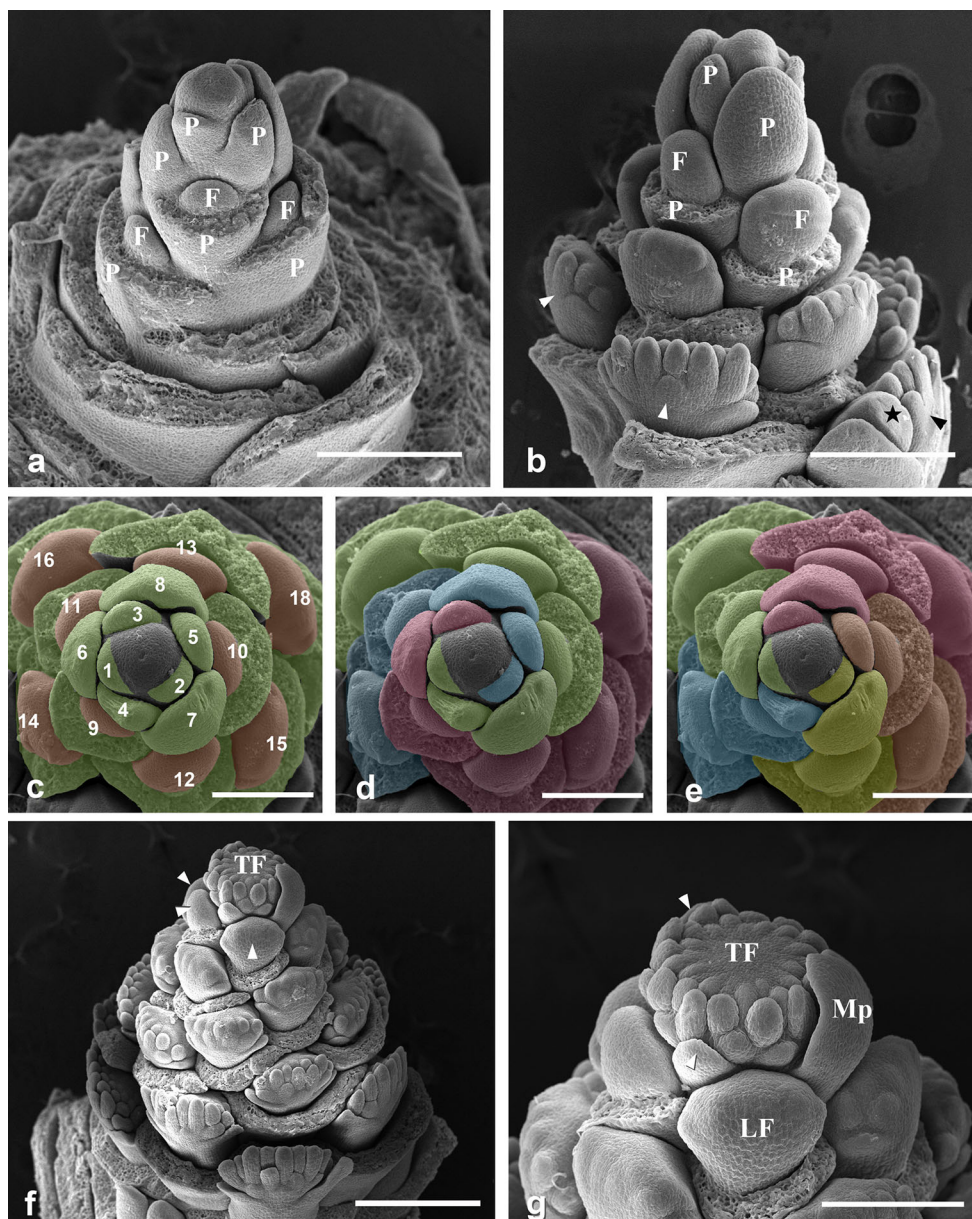


Fig. 3 *Trochodendron aralioides*. Development of young inflorescences. **a** A side view of a young inflorescence (July). After the excision of some perophylls subtending flowers (P), the young flowers (F) are shown in the axils of perophylls. **b** Side view of a young inflorescence (August). Some floral perophylls were removed to show that lateral flowers (indicated by *arrowheads*) develop earlier in the lower than in the upper parts. The lowermost lateral branch (secondary inflorescence) has an early developed secondary terminal flower (*black arrowhead*) and a small secondary lateral floral primordium (*star*) on the left side of the secondary terminal flower. **c** *Top view* of a young inflorescence with young flowers (*orange*) and perophylls (*green*) (July). The developmental sequence of

perophylls and young flowers is numbered (beginning with the youngest). **d, e** The same view as **c** showing the set of three parastichies (anticlockwise direction) and the set of five parastichies (clockwise direction). The young flowers and perophylls of the same parastichy are shown by the same colour. **f** Side view of an inflorescence at a later stage (September). The terminal flower (TF) developed earlier than the upper lateral flowers (*arrowheads*). **g** Close-up of **f** terminal flower with one large metaxyphyll (Mp) and two small metaxyphylls (*arrowheads*) and numerous young scales (rudimentary tepals) or stamens. *F* young flower, *LF* lateral flower, *Mp* metaxyphyll, *P* perophyll, *TF* terminal flower. *Bars a, b* = 300 μ m; *c-e* = 200 μ m. *Bars f* = 500 μ m; *g* = 200 μ m

the inflorescence primordia commonly occurs from June to July. From July to mid-September, many spirally arranged lateral flowers arise acropetally. When the terminal flower appears, the uppermost lateral flowers are not yet visible.

However, the number of flowers in an inflorescence is determined when the terminal flower appears. The floral organs appear first in the lower lateral flowers in about mid-July, at the beginning of stage 3. The development of

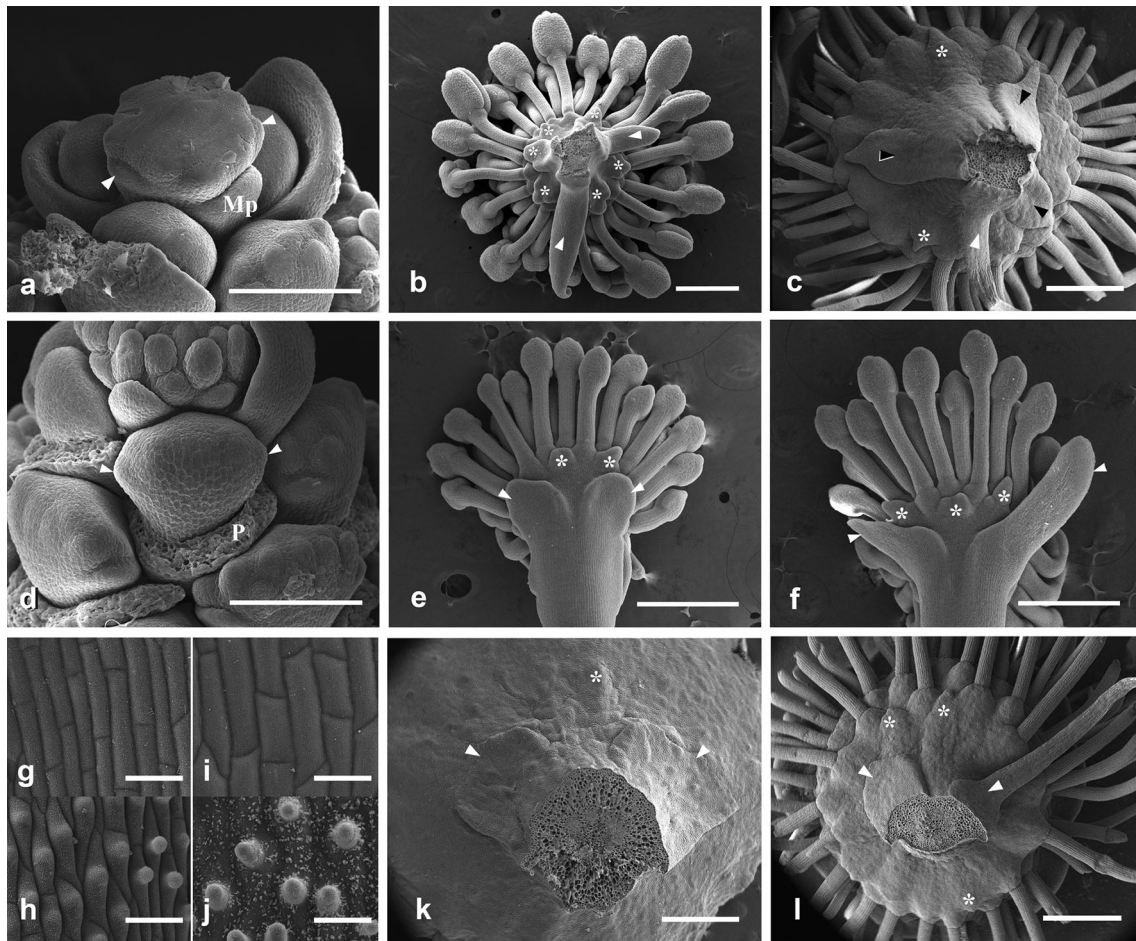


Fig. 4 *Trochodendron aralioides*. Development of a metaxyphyll in terminal flowers (**a–c**, **g**, **h**), pherophyll (subtending bract) and prophyll in lateral flowers (**d–f**, **i–l**). **a** Terminal young flower with metaxyphylls (Mp and arrowheads) (September). **b** Bottom view of a terminal flower with two large metaxyphylls (arrowheads) and several scales (asterisks) (January). Stamens develop into anthers and long filaments. **c** Bottom view of a terminal flower with linear metaxyphyll (white arrowhead), two triangular scales (black asterisks) and several scales (white asterisks) (March). The first metaxyphyll was excised. **d** Lateral flower with two prophyll primordia (arrowheads) (September). **e** Upper lateral flower with

two prophylls (arrowheads) and two tepal-like scales (asterisks) (October). **f** Lower lateral flower with two prophylls (arrowheads) and several scales (asterisks) in the same inflorescence as (**e**). **g** Adaxial epidermal cells of a metaxyphyll. **h** Abaxial epidermal cells of a metaxyphyll. **i** Adaxial epidermal cells of a pherophyll. **j** Abaxial epidermal cells of a pherophyll. **k** Bottom view of a lateral protogynous flower with two prophylls (arrowheads) and one scale (asterisk) (April). **l** Bottom view of a lateral protandrous flower with two prophylls (arrowheads) and several scales (asterisks) (March). **P** pherophyll. Bars **a** and **d** = 200 μm ; **b**, **e** and **f** = 200 μm ; **c**, **k**, **l** = 1 mm; **g–j** = 50 μm

floral organs occurs until early March of the second year. From mid-March to early April, the inflorescence becomes exposed, followed by the exposure of the flowers. Subsequently, anthers on flowers of protandrous individuals are the first to shed pollen grains; stigmas on flowers of protogynous individuals are receptive. About 1 week after the stigmas of protogynous flowers become receptive, their anthers begin to shed pollen grains. The stigmas of protandrous flowers remain receptive until all anthers have finished releasing pollen grains. By May, all flowering has finished and fruits start to develop. Fruits usually mature and release seeds from October of the second year to April of the third year.

Discussion

Reproductive cycles and inflorescence type

In angiosperms, the length of the reproductive cycle of adult flowering plants ranges from about 26 days, e.g. *Arabidopsis* (Smyth et al. 1990), to many months (Bonner 2008), from the initiation of reproductive buds to maturation of the seeds. In *T. aralioides*, it takes about 9 months for the flowers to develop, and fruits mature in the following autumn (Baskin et al. 2006). The reproductive cycle of *T. aralioides* has a 2-year reproductive cycle that is common for many trees (Owens and Blake 1985) in the temperate zone.

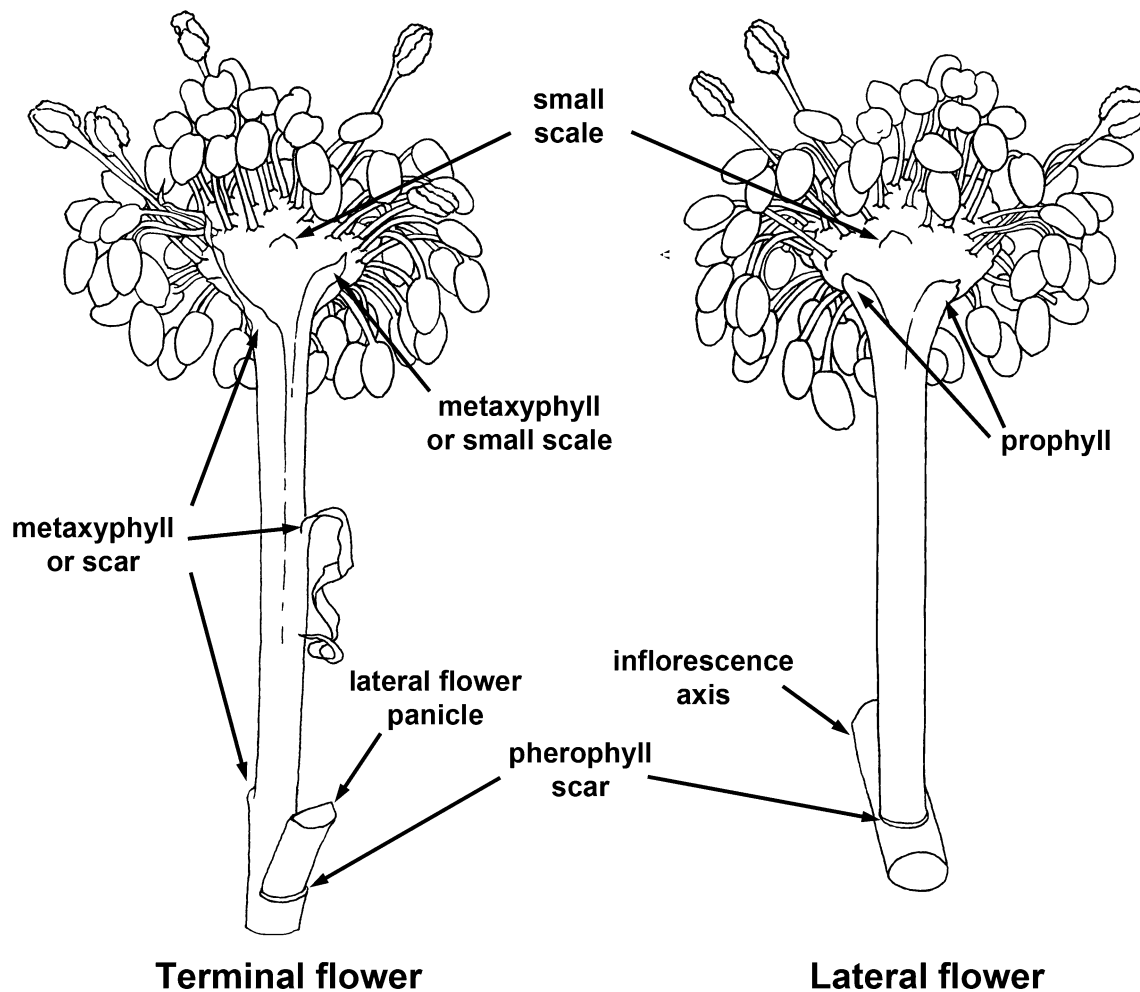


Fig. 5 *Trochodendron aralioides*. Diagram of bracts and residual perianth on the pedicel and receptacle of terminal and lateral anthetic flowers

The present study confirms that the inflorescence of *T. aralioides* is a botryoid (Weberling 1981). Sometimes there are one or two secondary lateral flowers at the base (as also observed by Endress 1986) which could be described as a poorly branched panicle. Botryoids and panicles often have metaxyphylls (Briggs and Johnson 1979; Weberling 1981) and they are present in *Trochodendron*. Within basal eudicots, inflorescences are variously differentiated; a botryoid or panicle is, however, also found in Lardizabalaceae, Berberidaceae and Buxaceae (Feng and Lu 1998; Endress and Igersheim 1999; von Balthazar and Endress 2002a; Harms 2007; Zhang and Ren 2011).

Sterile bract morphology

Most eudicot flowers are supported by a pherophyll (subtending leaf of bract) and most are preceded by a pair of

lateral prophylls (bracteoles) (Ronse De Craene 2010). The metaxyphylls, on the other hand, are sterile bracts—“empty” phyllomes that are positioned below the terminal flower (Briggs and Johnson 1979; Weberling 1981). In *Trochodendron*, the pherophylls and metaxyphylls protect flowers in early development, but the prophylls are relatively small and do not have a noticeable protective function. In *Tetracentron*, the pherophyll is small and two pairs of tepals protect the young floral organs (Endress 1986; Chen et al. 2007; Gan et al. 2013).

In *Trochodendron*, the prophylls have variable shapes and sizes and are larger in association with the lowermost lateral flower (Endress 1986). The shape and size of the metaxyphylls also vary. The abaxial epidermal cells are papillate in the floral bracts and pherophyll (Wu et al. 2007). Furthermore, the cells of the abaxial epidermis in the metaxyphylls are papillate; thus, the epidermal cell morphology among these sterile bracts is similar.

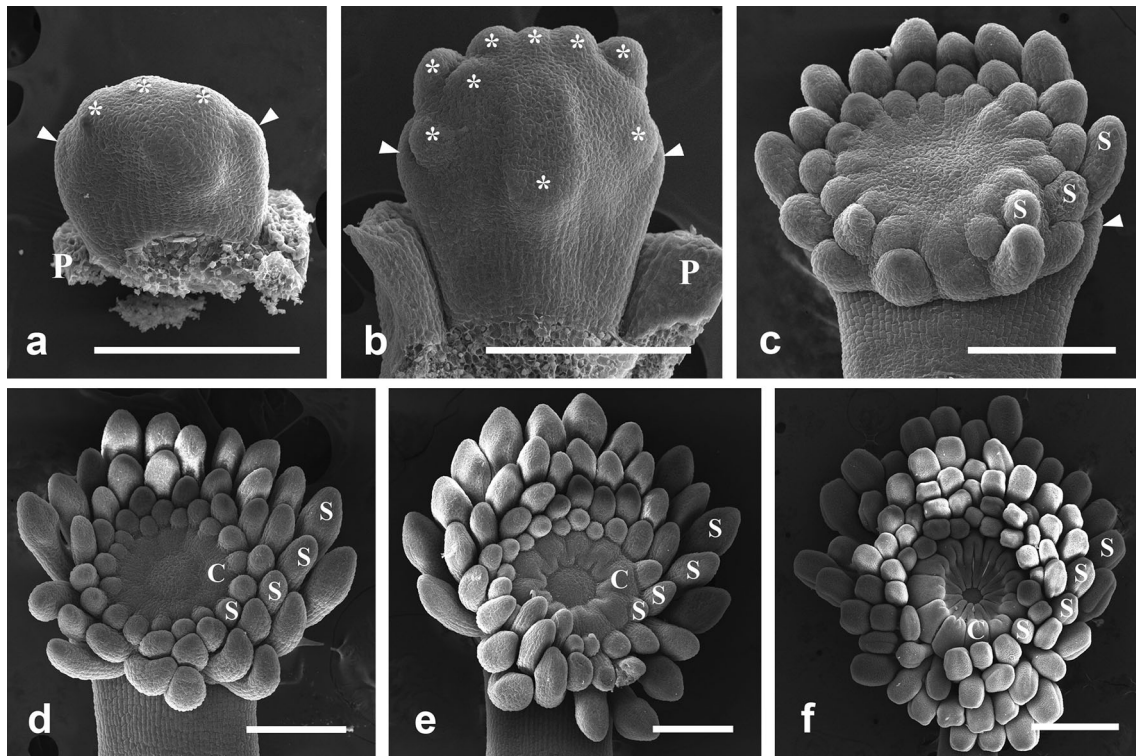


Fig. 6 *Trochodendron aralioides*. Development of lateral flowers viewed from the adaxial side. **a** Flower with two prophyll primordia (arrowheads) and some inconspicuous bulges, which are the primordia of small scales (rudimentary tepals) or stamens (asterisks) (September). **b** Flower with two young prophylls (arrowheads) and primordia of small scales or stamens (September). Development is

delayed on the adaxial side. **c** Flower with young stamens (September). **d** The carpel primordia appear in a single series in the centre of the flower (September). **e** Adaxial part of each young carpel concave (September). **f** Ventral slit of carpels closed (December). *P* prophyll; *S* stamen; *C* carpel. Bars **a–e** = 200 μm; **f** = 500 μm

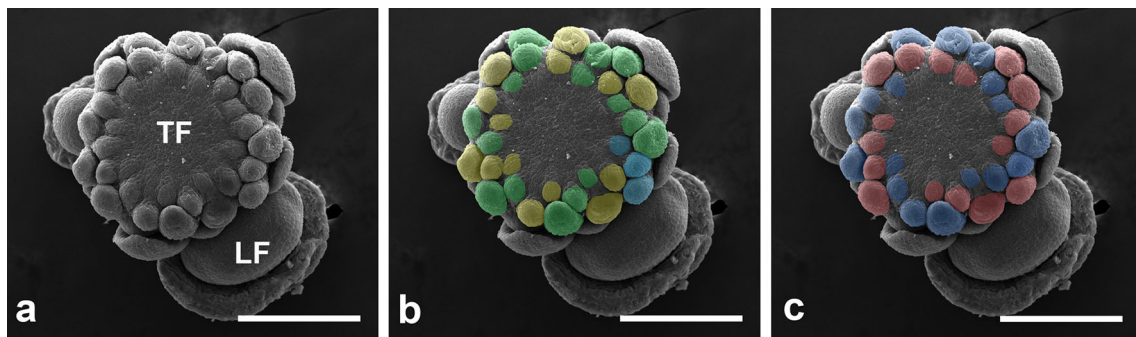


Fig. 7 *Trochodendron aralioides*. Terminal flower with spiral phyllotaxis (September), top view. **a** Flower with stamens unmarked. **b–c** Stamens are coloured to show the parastichy sets of 13 and 8 (clockwise and anticlockwise). *TF* terminal flower; *LF* lateral flower. Bars **a–c** = 200 μm

Floral phyllotaxis and floral organ morphology

In lateral *T. aralioides* flowers, the delayed development of the abaxial side causes early monosymmetry (Pervukhina and Yoffe 1962; Endress 1986) and a reduction in the number of stamens. However, the terminal flower is radially symmetrical. The terminal flower is preceded by three

or more metaxyphylls and several small scales between the metaxyphylls and the stamens. It is difficult to distinguish metaxyphylls from small scales by their morphology and they vary continuously in shape. The small scales are assumed to be rudimentary perianth organs (Endress 1986). Additional detailed developmental studies are necessary in order to better understand the rudimentary perianth.

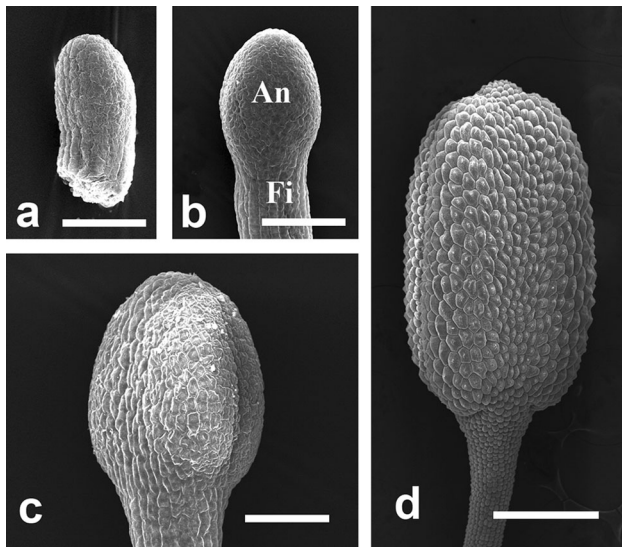


Fig. 8 *Trochodendron aralioides*. Development of stamens. **a** A young, rod-shaped stamen (October). **b** Stamens already differentiated into anther (An) and filament (Fi) (October). **c** Anther enlarged and having four pollen sacs (October). **d** Anther shortly before anthesis. An anther; Fi filament. Bars **a–c** = 50 μm ; **d** = 500 μm

At the early stages, the terminal flower of *T. aralioides* has a flat receptacle, and thus, phyllotaxis is more easily observed than in lateral flowers or in terminal flowers at a later stage. Androecium phyllotaxis in the early stages is spiral or almost whorled, also described by Endress (1986), and approximately whorled flowers were also found (Endress 1990).

Carpel development and morphology of *Tetracentron* and *Trochodendron* are similar, which was previously shown and discussed in Endress (1986). The young carpels of *Tetracentron* are formed within a limited space and are squeezed by the stamens. In contrast, the young carpels of *Trochodendron* have more room for development (Chen et al. 2007). Unicellular papillate stigmas are found in Trochodendrales and in some other basal eudicots such as Platanaceae (Endress and Igersheim 1999), Didymelaceae (von Balthazar et al. 2003) and Buxaceae (von Balthazar and Endress 2002a, b). The bottle-shaped unicellular stigmatic papillae and the long decurrent stigma in two crests in Trochodendrales are also observed in Buxales (von Balthazar and Endress 2002b). In Trochodendraceae, the

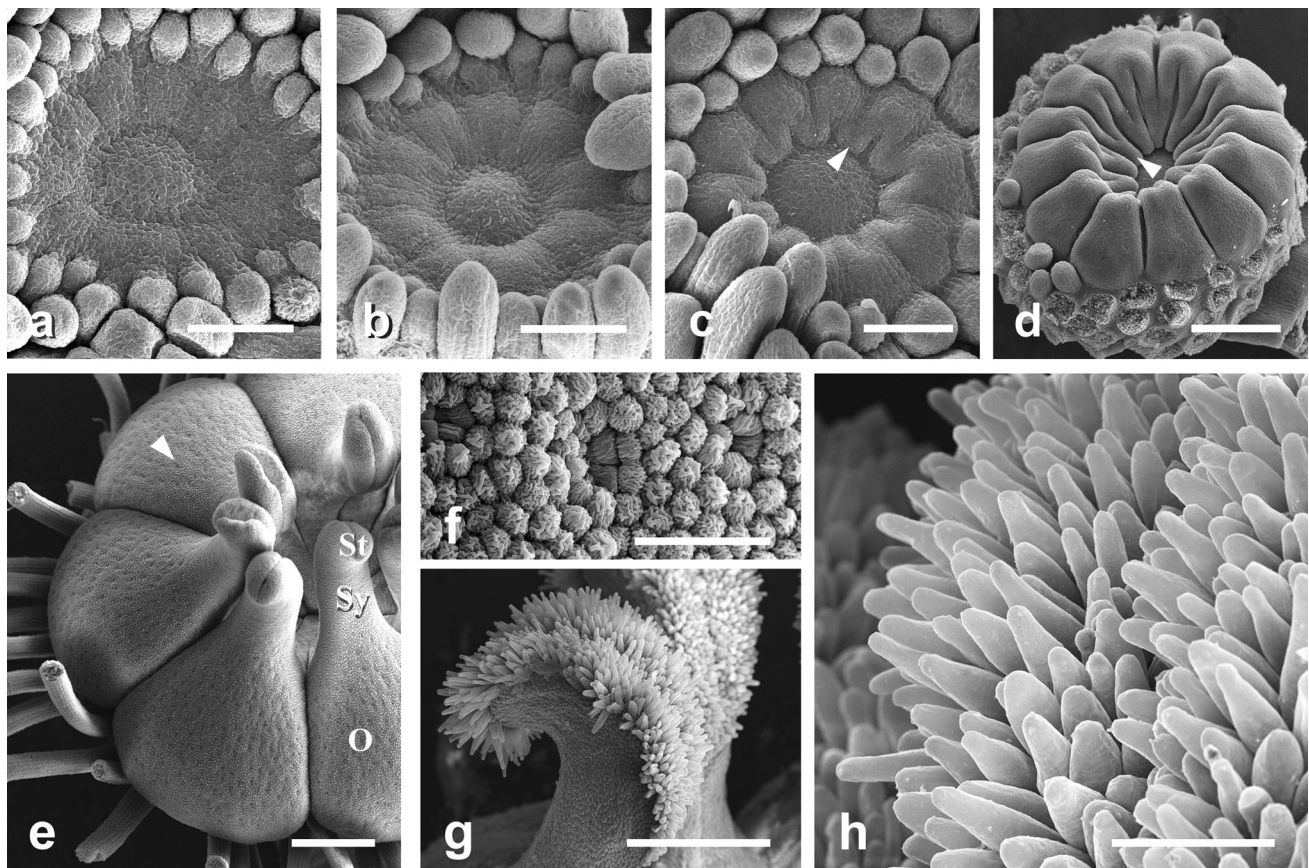


Fig. 9 *Trochodendron aralioides*. Development of carpels. **a**, **b** Young carpels arise in a series (September). **c**, **d** Carpels become plicate (September, December), and the basal edges of neighbouring carpels fuse (arrowhead). **e** Carpels of protandrous flower in front

view at anthesis. There are nectaries on the abaxial side of the carpel (arrowhead) (March). **f** Nectary with stoma. **g** Expanded unicellular papillate stigma. **h** Unicellular papillae. O ovary; St stigma; Sy style. Bars **a–c**, **h** = 100 μm ; **d** = 200 μm ; **e**, **g** = 500 μm ; **f** = 50 μm

Table 1 Stages of inflorescence and flower development in *Trochodendron aralioides*

	First year						Second year						
	Month	6	7	8	9	10	11	12	1	2	3	4	5
Stage 1		Inflorescence primordium formation											
Stage 2		Floral primordium formation											
Stage 3		Floral organ development											
Stage 4								Anthesis					

plicate carpels with bottle-shaped unicellular papillate stigmas and dimerous carpel development of *Tetracentron* are indicators of its relationship with the Buxales (Chen et al. 2007) and other basal eudicots.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical statement The authors comply will all rules of the journal following the COPE guidelines; all authors have contributed and approved the final manuscript.

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