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Flower morphology and relationships of *Schefflera subintegra* (Araliaceae, Apiales): an evolutionary step towards extreme floral polymery

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Gross morphology and the development of flowers in *Schefflera subintegra* (Araliaceae) are examined. The floral groundplan of this species is found to be very similar to that of *Tupidanthus calyptratus* representing a case of most extreme floral polymery within Araliaceae. *Schefflera subintegra* differs from *T. calyptratus* with respect to a lower floral merism (19–43 versus 60–172 stamens and 15–33 versus 60–138 carpels respectively) and by transformation from polysymmetry to disymmetry of flower in the course of its development. Close relationships between *S. subintegra*, *T. calyptratus*, and *Schefflera hemiepiphytica* have been confirmed by phylogenetic analysis based on nuclear ribosomal internal transcribed spacer sequences. These species form a subclade within the Asian *Schefflera* clade, with *T. calyptratus* as a sister taxon to two other species. Apart from more or less pronounced floral polymery, the species of this subclade share calyx and corolla without any traits of individual sepals and petals, and also a massive calyptra. As these data suggest, the extremely polymerous flowers of *Tupidanthus* apparently evolved in two steps: (1) the saltational multiplication of floral elements together with a loss of individuality of sepals in the calyx and petals in the corolla and (2) further polymerization of androecium and gynoecium. Mutation(s) in *CLAVATA*-like gene(s) are suggested as a possible mechanism of the saltation event. © 2014 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2014, **175**, 553–597.

ADDITIONAL KEYWORDS: calyptra – *CLAVATA* gene family – evo-devo – fasciation – flower – *Scheffleropsis* – taxonomy.

INTRODUCTION

Araliaceae are unusual among euasterids (APG III, 2009) in their extreme diversity of floral morphology. Most members of Araliaceae share tetracyclic pentamerous flowers (often with a dimerous gynoecium) that are also typical for related groups in the order Apiales and for other taxa of the euasterid clade (Endress, 1990, 2010, 2014; Ronse De Craene & Smets, 1994). However, conspicuous deviations from this floral groundplan, such as multiplication of stamen whorls or shifts from pentamerous to tetra- or polymerous whorls, occur in some lineages of Araliaceae (Philipson, 1970; Eyde & Tseng, 1971; Frodin,

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1975; Sokoloff *et al*., 2007; Nuraliev, Beer & Oskolski, 2009; Nuraliev *et al*., 2010; Oskolski *et al*., 2010a, 2011; Nuraliev, Sokoloff & Oskolski, 2011; Nuraliev, 2012). Among these deviations, high floral merism has traditionally been considered as a primitive condition for the family (Bentham, 1867; Clarke, 1879; Harms, 1898; Viguier, 1906; Li, 1942; Tikhomirov, 1961; Melchior, 1964; Takhtajan, 1966, 1987; Philipson, 1970; Eyde & Tseng, 1971; Grushvitzky & Skvortsova, 1973; Grushvitzky, 1981). According to another view (Cronquist, 1968, 1981, 1988), which is currently commonly accepted (Plunkett, 2001; Lowry, Plunkett & Wen, 2004; Plunkett *et al*., 2005; Jabbour, Damerval & Nadot, 2008; Takhtajan, 2009), polymerous flowers are not primitive in Araliaceae. Rather, multiple gains of floral polymery took place in the family (Nuraliev *et al*., 2010).

The most aberrant floral groundplan in Araliaceae occurs in *Tupidanthus calyptratus* Hook.f. & Thomson, a species distributed from northern India (Assam) to south-eastern China (Yunnan) and northern Indo-China (Eyde & Tseng, 1971; Grushvitzky, 1981; Wen *et al*., 2001; Shang & Lowry, 2007; Sokoloff *et al*., 2007; Nuraliev *et al*., 2009; Konstantinova & Suchorukow, 2010). *Tupidanthus calyptratus* was shown to be nested within the Asian clade of the large and polyphyletic genus *Schefflera* J.R.Forst. & G.Forst. (Plunkett *et al*., 2005; Li & Wen, 2013). This makes it essential to analyze the floral morphology of the taxa in the phylogenetic surrounding of this species.

In the present study, we focus on floral morphology and phylogenetic relationships of *Schefflera subintegra* (Craib) C.B.Shang, an Asian species of *Schefflera* with a considerably deviating floral groundplan, regarded by many authors to be a close relative of *T. calyptratus* (Frodin, manuscript, cited by Eyde & Tseng, 1971; Grushvitzky & Skvortsova, 1973; Grushvitzky *et al*., 1985; Grushvitzky, Skvortsova & Ha Thi Dung, 1988; Plunkett *et al*., 2005; Frodin, Lowry & Plunkett, 2010; Konstantinova & Suchorukow, 2010). Detailed descriptions of flower structure and development based on fixed material are so far lacking for this key taxon.

Schefflera subintegra and three other Asian *Schefflera* spp. have sometimes been segregated as the separate genus *Scheffleropsis* Ridl. (Grushvitzky & Skvortsova, 1973; Grushvitzky *et al*., 1985, 1988; Takhtajan, 2009), which is currently not accepted by most researchers (Frodin & Govaerts, 2004; Plunkett *et al*., 2005; Frodin *et al*., 2010; Konstantinova & Suchorukow, 2010). This genus has sometimes been considered to represent an evolutionary link between *Tupidanthus* Hook.f. & Thomson and *Schefflera* (Grushvitzky & Skvortsova, 1973). So far, however, the hypothesis regarding their close relationships has not been tested in detail using molecular phylogenetic data.

Although the derived nature of floral polymery in Araliaceae is currently well supported by various kinds of data, the precise pathways of flower evolution remain obscure as a result of insufficient information on floral morphology and development and species relationships. With respect to the Asian *Schefflera* clade (including *Tupidanthus*), the main questions are: (1) what are the relationships between species with polymerous flowers in the clade and how many times did floral polymery evolve in this group; (2) is the evolution of floral merism correlated with evolution of any other floral features; and (3) what are the functional and ecological implications of various deviations from the typical araliaceous floral groundplan? In the present study, we aim to fill some gaps related to the first two questions; the last and probably the most enigmatic question remains to be investigated. The present study is a continuation of a series of papers on reproductive morphology and biology of Araliaceae (Sokoloff *et al*., 2007; Nuraliev *et al*., 2009, 2010, 2011; Oskolski, Sokoloff & van Wyk, 2010b; Nuraliev, 2012, 2013).

Background: taxonomic position, species delimitation, and evolutionary interpretation of *Schefflera subintegra*, *Tupidanthus calyptratus*, and their proposed relatives

Current views on T. calyptratus

This has long been assumed to be a key species for understanding evolution of Araliaceae as a result of its outstanding floral morphology. Its flowers have up to 172 stamens and 138 carpels (Sokoloff *et al*., 2007). Reportedly, carpel number in *Tupidanthus* can be as high as 200 (Grushvitzky, 1981; Wen *et al*., 2001) or even more (Eyde & Tseng, 1971). Moreover, the outline of organ insertion is irregularly undulating in all four floral whorls (i.e. calyx, corolla, androecium, and gynoecium) in *T. calyptratus*, probably as a result of folding of the entire receptacle. Finally, its calyx is represented by an extremely short tube without any traits of individual sepals, and the corolla forms a massive calyptra, the individual petals of which cannot be distinguished (Sokoloff *et al*., 2007; Nuraliev *et al*., 2009, 2011).

As the molecular, morphological and biogeographical data suggest (Oskolski, 1995; Plunkett & Lowry, 2001; Wen *et al*., 2001; Lowry *et al*., 2004; Plunkett, Wen & Lowry, 2004; Plunkett *et al*., 2005; Frodin *et al*., 2010; Konstantinova & Suchorukow, 2010; Li & Wen, 2013), the monospecific genus *Tupidanthus* is closely related to Asian species of the large and polyphyletic genus *Schefflera*. For this reason, *T. calyptratus* was reconsidered by Lowry, Miller & Frodin (1989) as *Schefflera pueckleri* (K.Koch) Frodin. In the last version of Frodin's informal system of *Schefflera*

(Frodin *et al*., 2010), this species belongs to subgroup '*Tupidanthus* 1' of the '*Brassaia*' group. This position of *Tupidanthus* in the Asian *Schefflera* clade is confirmed by molecular phylogenetic data (Plunkett *et al*., 2005).

Although the majority of members of the Asian *Schefflera* clade share tetracyclic, pentamerous flowers with free petals, some of them have flowers that form a series linking this typical groundplan and the unusual flower of *Tupidanthus*. Thus, this group would provide a convenient model for studies of evolutionary shifts in floral merism.

History of the genus Scheffleropsis

The first species of the *Scheffleropsis* group was described by Ridley (1917) from peninsular Malaysia as *Schefflera polyandra* Ridl. Later, he segregated this species into a newly described monospecific genus *Scheffleropsis* Ridl. and consequently proposed a new combination, *Scheffleropsis polyandra* (Ridl.) Ridl. (Ridley, 1922). Ridley stated that the new genus resembles *Schefflera* but has serrate leaflets and numerous (14–16) stamens and an eight-celled ovary. According to Ridley (1917, 1922), *Scheffleropsis polyandra* has a calyptrate corolla of five petals. Ridley (1922) placed *Scheffleropsis* just before *Tupidanthus* in a linear sequence of genera.

Craib (1930) described the second species of the genus, *Scheffleropsis subintegra* Craib, from peninsular Thailand. He placed this species within tribe Plerandreae. Craib's material possessed flowers with 20 stamens, 15 carpels, and a calyptrate corolla. A year later, the same author described *S. subintegra* var. *angkae* Craib from a fruiting tree found in the northern Thailand, which was characterized by the gynoecium of 18 carpels (Craib, 1931).

Frodin (manuscript, cited by Eyde & Tseng, 1971) suggested that *Scheffleropsis* should not be segregated from *Schefflera*. He considered *Scheffleropsis subintegra* to be a species of *Schefflera* most closely related to *Tupidanthus calyptratus*. In general, after publications by Craib, the genus *Scheffleropsis* was almost neglected by botanists until the detailed revision by Grushvitzky & Skvortsova (1973).

Grushvitzky & Skvortsova (1973) followed Craib (1930) and classified *Scheffleropsis* in tribe Plerandreae. The tribe was characterized by supposedly primitive features such as polymerous flowers and calyptrate corolla and included also *Plerandra* A.Gray, *Trevesia* Vis and *Tupidanthus* (Grushvitzky & Skvortsova, 1973; Grushvitzky *et al*., 1985, 1988). Besides the floral polymery, Grushvitzky & Skvortsova (1973) considered some other floral traits such as the calyptrate corolla and multiple vascular bundles in stamens to be common for *Scheffleropsis* and *Tupidanthus* (although these features are found not in all of four species of *Scheffleropsis*). In this classification, *Schefflera* was viewed as a member of a more advanced tribe Scheffllereae (Grushvitzky *et al*., 1985).

Grushvitzky & Skvortsova (1973) summarized arguments for recognizing *Scheffleropsis* as a genus distinct from *Schefflera*. They found the following diagnostic features of *Scheffleropsis*: flowers in lax lateral panicles of umbels; short calyx; corolla of eight petals most often joined into calyptra; a one-whorled androecium of eight to 28 stamens, which, in most species, leave distinct scars after abscission; and a gynoecium of eight to 23 carpels. Apart from the two previously recognized species (*S. polyandra* and *S. subintegra*), two other species were accepted. *Scheffleropsis angkae* (Craib) Grushv. & Skvortsova was based on *S. subintegra* var. *angkae*. According to Grushvitzky & Skvortsova (1973), it differs from *S. subintegra s.s.* by flowers with 23–27 (rather than 16–22) stamens and 20–23 (rather than 14–20) carpels and by its oblongly elliptic to oval (rather than rounded) style. However, the flowers of *S. angkae* were not examined and all their conclusions about the floral structure were based on examination of fruits. According to Grushvitzky & Skvortsova (1973, fig. 5), the stamen scars are narrowly elliptic in *S. subintegra* (and also in *S. polyandra*), whereas they are rounded in *S. angkae*. For type specimens of both *S. subintegra* and S. *angkae*, Grushvitzky & Skvortsova (1973) report the petal number in the calyptra based on their own observations. Another new species, *Scheffleropsis hemiepiphytica* Grushv. & Skvortsova, was described from two locations in northern Vietnam (Grushvitzky & Skvortsova, 1973). According to Grushvitzky & Skvortsova (1973), *S. hemiepiphytica* differs from the other species of *Scheffleropsis* by its hemiepiphytic habit, large leaves (length of up to 90 cm), woody persistent bracts, gynoecium with short apically free styles, and hairy stigmas. The hemiepiphytic plant was considered as epiphytic with aerial roots reaching the soil (i.e. primary hemiepiphyte; Zotz, 2013). The material of Grushvitzky & Skvortsova was in fruits; therefore, they did not have an opportunity to examine anthetic flowers. However, they were able to count androecium merism using stamen scars on the fruits. Thus, the flower of *S. hemiepiphytica* was reported to bear (19)20–21(22) stamens and (8)10–11(13) carpels.

Grushvitzky & Skvortsova (1973) divided *Scheffleropsis* into two sections. Section *Scheffleropsis* included the only species *S. polyandra* and was characterized by serrate leaflet margins, subulate ligules, isomerous flowers with eight elements in each whorl (including calyptrate corolla), and stamen filaments with single vascular bundles. Stamen filaments of *S. polyandra* are reported not to leave distinct scars after abscision, although neither fruits, nor anthetic or post-anthetic flowers were known. As the authors found, some of flower buds in the type material of *S. polyandra* show opening of the corolla with spreading petals (i.e. without formation of a calyptra). Grushvitzky & Skvortsova (1973) showed that the original data of Ridley (1922) on the absence of isomery in flowers of *S. polyandra* were incorrect.

Section *Integrifoliae* Grushv. & Skvortsova included the other three species and was characterized by entire leaflet margin, cupuliform ligule, flowers with stamen and carpel number exceeding petal number, and stamen filaments with three vascular bundles. In addition, Grushvitzky & Skvortsova (1973) noted that, in all species of section *Integrifoliae*, and in contrast to *S. polyandra*, stamens leave distinct scars after abscission. Because of the peculiarities of the flower structure of *S. polyandra*, it was considered as an intermediate species between *Schefflera*opsis and *Schefflera* and between tribes Plerandreae and Schefflereae. Grushvitzky & Skvortsova (1973) suggested close relationships between *S. hemiepiphytica* and *Schefflera tunkinensis* R.Vig. According to Grushvitzky & Skvortsova (1973), these two species share lateral (in our view, presumably pseudolateral) inflorescences, woody floral buds and a number of common vegetative features.

Grushvitzky & Skvortsova (1973) did not take into account the type of fusion between adjacent petals in calyptrate corollas of Araliaceae. They assumed the calyptrate corolla to be a common feature of *Tupidanthus*, *Schefflera*opsis, *Plerandra s.s.*, *Tetraplasandra* A.Gray, and *Trevesia*. As we currently know, *Tupidanthus* has congenitally united petals, whereas the calyptrate corollas of *Plerandra*, *Tetraplasandra* (now synonymized with *Polyscias* J.R.Forst. & G.Forst.), and *Trevesia* are formed by postgenital petal fusion (Nuraliev *et al*., 2010). The difference between these two modes of fusion (congenital and postgenital) are morphologically and evolutionally more crucial than the differences between free and postgenitally united floral elements (Leinfellner, 1950; Verbeke, 1992; Sokoloff *et al*., 2006) and, for this reason, using the presence or absence of a calyptra (irrespectively of its structure) as a taxonomic character is not correct.

Shang (1984) treated *Schefflera*opsis as a synonym of *Schefflera*. He accepted, however, all four species (under appropriate combinations) recognized by Grushvitzky & Skvortsova (1973) in the former taxon. The most recent taxonomic treatments of *Schefflera* and related taxa were conducted by Frodin and collaborators (Frodin & Govaerts, 2004; Plunkett *et al*., 2005; Frodin *et al*., 2010). In Frodin's informal system of *Schefflera*, the genus is interpreted extremely broadly and includes species of the former *Plerandra*, *Tupidanthus*, *Schefflera*opsis, and many other genera related to *Schefflera* in its traditional circumscription. *Schefflera pueckleri* (= *Tupidanthus calyptratus*), *S. hemiepiphytica* (Grushv. & Skvortsova) C.B.Shang, and *S. subintegra* are placed into the group '*Brassaia*', subgroup '*Tupidanthus* 1' of the last version of this system. *Schefflera angkae* (Craib) C.B.Shang and *Schefflera subintegra* var. *angkae* Craib are considered as synonyms of *S. subintegra* (Frodin & Govaerts, 2004). Although Frodin & Govaerts (2004) cited *Schefflera subintegra* var. *angkae*, this combination has never been published; it should probably be replaced with *Schefflera*opsis *subintegra* var. *angkae* Craib, which is not listed in their checklist.

Although *Schefflera polyandra* is currently accepted as a separate species (Frodin & Govaerts, 2004), it was classified by Frodin (Stone, 1978) as *Schefflera ridleyi* (King) R.Vig. var. *polyandra* (Ridl.) Frodin (which was not, however, validly published). By contrast to var. *polyandra*, var. *ridleyi* (which is also known from peninsular Malaysia) has isomerous hexamerous flowers. Notwithstanding the findings of Grushvitzky & Skvortsova (1973), Frodin followed Ridley (1922) in assuming the androecium of var. *polyandra* as 14–16-merous; the petal number was not indicated (Stone, 1978). *Schefflera ridleyi* belongs to the group '*Parapanax*', subgroup '*Parapanax*' of Frodin's informal system of *Schefflera* (Stone, 1978; Plunkett *et al*., 2005; Frodin *et al*., 2010). Despite other classifications, Frodin's treatment suggested polyphyly of *Schefflera*opsis *sensu* Grushvitzky & Skvortsova (1973).

MATERIAL AND METHODS

In naming the material studied in the present paper, we follow Frodin's (Frodin & Govaerts, 2004) broad concept of *Schefflera subintegra* with rejection of its varieties (i.e. with inclusion of *S. angkae* = *Schefflera*opsis *subintegra* var. *angkae* into *S. subintegra*).

Herbarium collections in E (isotype of *Schefflera siamensis* W.W.Sm. ex Craib, accessed online), HN (*S. angkae*; *S. hemiepiphytica*, including the type specimen and a paratype; *S. subintegra*), K (*S. hemiepiphytica*, including isotype; *S. ridleyi s.l.*, including its type and the type of *S. polyandra*; *S. siamensis*, including its type; *S. subintegra*, including its isotype and type of *S. angkae*), LE (*S. angkae*; *S. hemiepiphytica*, including a paratype), P (*S. subintegra*, accessed online) and SING (*S. polyandra*, *S. ridleyi*, *S. subintegra*) were examined.

For morphological and morphogenetic investigations, inflorescences and flowers at various developmental stages were fixed and stored in 70% ethanol. Floral samples were taken from plants of *S. subintegra* collected in northern Thailand [*M. S. Nuraliev*, *I. A. Savinov no. 5* (Table 1)], north-eastern Thailand [*M. S. Nuraliev*, *I. A. Savinov nos. 58 and 59* (Table 1)

Table 1. Voucher information and GenBank accession numbers for sequences used in the present study

Species and specimens	Source or voucher information	Genank number
Heteropanax fragrans (Roxb.) Seem.	Wen *et al*. (2008)	DQ007377
Schefflera actinophylla (Endl.) Harms (listed as *Brassaia actinophylla* Endl.)	Wen *et al*. (2001)	AF242245
Schefflera arboricola (Hayata) Merr.	Wen *et al*. (2001)	AF242243
Schefflera bractescens Ridl.	Plunkett *et al*. (2005)	AY955448
**Schefflera brevipedicellata* Harms (1)	Vietnam, Lao Cai prov., Sa Pa distr., San Sa Ho municipality, Hoang Lien National Park, Cat Cat village area, N 22°19′32″, E 103°49′52″, 1210 m, 26.11.2009. *M. S. Nuraliev 42* (MW)	JF284834
**Schefflera brevipedicellata* (2)	Vietnam, Lao Cai prov., Sa Pa distr., San Sa Ho municipality, Hoang Lien National Park, Cat Cat village area, N 22°19′19″, E 103°49′33″, 1240 m, 16.12.2009. *M. S. Nuraliev 50* (MW)	JF284841
Schefflera delavayi (Franch.) Harms (1)	Plunkett *et al*. (2005)	EF152176
Schefflera delavayi (2)	Wen *et al*. (2008)	DQ007391
Schefflera delavayi (3)	Plunkett *et al*. (2005)	AY955450
Schefflera aff. *dentata* Frodin ex P.Royen	Plunkett *et al*. (2005)	AY955451
Schefflera elliptica (Blume) Harms (1)	Plunkett *et al*. (2005)	AY955453
Schefflera elliptica (2)	Plunkett *et al*. (2005)	AY955452
Schefflera fantsipanensis Bui (1)	Plunkett *et al*. (2005)	AY955455
**Schefflera fantsipanensis* (2)	Vietnam, Lao Cai prov., Sa Pa distr., San Sa Ho municipality, Hoang Lien National Park, Tram Ton area, N 22°21′11″, E 103°46′30″, 1950 m, 07.06.2009. *M. S. Nuraliev 6* (MW)	JF284824
**Schefflera fantsipanensis* (3)	Vietnam, Lao Cai prov., Sa Pa distr., San Sa Ho municipality, Hoang Lien National Park, Tram Ton area, N 22°19′53″, E 103°46′54″, 2150 m, 09.06.2009. *M. S. Nuraliev 10* (MW)	JF284825
**Schefflera fantsipanensis* (4)	Vietnam, Lao Cai prov., Sa Pa distr., San Sa Ho municipality, Hoang Lien National Park, Tram Ton area, N 22°19′53″, E 103°46′54″, 2150 m, 09.06.2009. *M. S. Nuraliev 11* (MW)	JF284821
**Schefflera hemiepiphytica* (Grushv. & Skvortsova) C. B. Shang	Vietnam, Hoa Binh prov., reg. Tuly, mt. Mieng, 300 m, 22.12.1969. *I. V. Grushvitzky*, *N. N. Arnautov*, *Pham Van Nguyen*, *Ha Thi Dung*, *Phan Ke Lok*, *Mai Nghi*, *So Va Ni 178* (sample from wood collection of Komarov Botanical Institute, voucher specimen, LE)	KF134666
Schefflera heptaphylla (L.) Frodin (1)	Plunkett *et al*. (2005)	AY955459
**Schefflera heptaphylla* (2)	China, Shenzhen, Fairy Lake Botanical Gardens, 27.09.2005. *A. A. Oskolski 705* (LE)	JF284844
Schefflera heterophylla (Wall. ex G.Don) Harms (1)	Wen *et al*. (2008)	DQ007388
Schefflera heterophylla (2)	Wen *et al*. (2008)	GU054642
Schefflera hullettii (King) R.Vig.	Wen *et al*. (2008)	DQ007392
Schefflera hypoleuca (Kurz) Harms (1)	Pandey, Wen & Pathak (2004)	AY725127
Schefflera hypoleucoides Harms (1)	Pandey *et al*. (2004)	AY725129
Schefflera hypoleucoides (2)	Pandey *et al*. (2004)	AY725128
Schefflera hypoleucoides (3)	Plunkett, Lowry & Burke (2001)	AF229732
**Schefflera hypoleucoides* (4)	Thailand, Chiang Mai prov., Mae Chaem distr., Doi Inthanon National Park, summit area, N 18°35′10″, E 98°29′00″, 2300–2500 m, 07.02.2009. *M. S. Nuraliev*, *I. A. Savinov 3* (MW)	JF284819

Table 1. *Continued*

Species and specimens	Source or voucher information	Genank number
**Schefflera hypoleucoides* (5)	Thailand, Chiang Mai prov., Mae Chaem distr., Doi Inthanon National Park, summit area, N 18°35′, E 98°30′, 2300–2500 m, 08.02.2009. *M. S. Nuraliev*, *I. A. Savinov 4* (spirit collection at Department of Higher Plants, Moscow State University)	JF284835
**Schefflera hypoleucoides* (6)	Vietnam, Lao Cai prov., Sa Pa distr., San Sa Ho municipality, Hoang Lien National Park, Tram Ton area, N 22°20′55″, E 103°47′20″, 1700 m, 20.06.2009. *M. S. Nuraliev 12* (MW)	JF284833
**Schefflera hypoleucoides* (7)	Vietnam, Lao Cai prov., Sa Pa distr., San Sa Ho municipality, Hoang Lien National Park, Tram Ton area, N 22°20′55″, E 103°47′20″, 1700 m, 20.06.2009. *M. S. Nuraliev 13* (MW)	JF284843
**Schefflera hypoleucoides* (8)	Vietnam, Lao Cai prov., Sa Pa distr., San Sa Ho municipality, Hoang Lien National Park, Cat Cat village area, N 22°20′00″, E 103°49′30″, 1300 m, 17.12.2009. *M. S. Nuraliev 53* (MW)	JF284837
**Schefflera hypoleucoides* (9)	Vietnam, Lao Cai prov., Sa Pa distr., San Sa Ho municipality, Hoang Lien National Park, road from O Qui Ho to Thac Bac, N 22°21′43″, E 103°47′20″, 1700 m, 18.12.2009. *M. S. Nuraliev 54* (MW)	JF284836
**Schefflera incisa* R.Vig.	Russia, St Petersburg, cultivated in the greenhouse # 20 of the Botanical Garden, the Komarov Botanical Institute (# 24300), 05.11.2013, *A. A. Oskolski 41-13* (MW)	JF284832
**Schefflera leucantha* R.Vig. (1)	Laos, Champasak Prov., Xe Pian National Protected Area, Phou Asa village area, N 14°45′50″, E 106°01′38″, 230 m, 25.01.2010. *M. S. Nuraliev*, *I. A. Savinov 62* (MW)	JF284830
**Schefflera leucantha* (2)	Thailand, Satun prov., Mueang Satun distr., Tarutao is., rocks along the sea, N 06°40′34″, E 99°38′24″, 17 m, 29.01.2010. *M. S. Nuraliev*, *I. A. Savinov 63* (MW)	JF284831
Schefflera aff. *lorentzii* Harms	Plunkett *et al*. (2005)	AY955461
Schefflera macrophylla (Dunn) R.Vig. (1)	Plunkett *et al*. (2001)	AF229733
**Schefflera macrophylla* (2)	Vietnam, Lao Cai prov., Sa Pa distr., San Sa Ho municipality, Hoang Lien National Park, Tram Ton area, N 22°21′11″, E 103°46′30″, 1950 m, 07.06.2009. *M. S. Nuraliev 8* (MW)	JF284820
**Schefflera membranifolia* Bui (1)	Vietnam, Lao Cai prov., Sa Pa distr., San Sa Ho municipality, Hoang Lien National Park, Tram Ton area, N 22°20′36″, E 103°45′56″, 2000 m, 29.06.2009. *M. S. Nuraliev 17* (MW)	JF284845
**Schefflera membranifolia* (2)	Vietnam, Lao Cai prov., Sa Pa distr., San Sa Ho municipality, Hoang Lien National Park, Tram Ton area, N 22°20′36″, E 103°45′56″, 2000 m, 29.06.2009. *M. S. Nuraliev 18* (MW)	JF284822
**Schefflera membranifolia* (3)	Vietnam, Lao Cai prov., Sa Pa distr., San Sa Ho municipality, Hoang Lien National Park, Tram Ton area, N 22°20′36″, E 103°45′56″, 2000 m, 29.06.2009. *M. S. Nuraliev 20* (MW)	JF284823
Schefflera microphylla Merr.	Wen *et al*. (2008)	DQ007389
Schefflera minutistellata Merr. ex H. L. Li	Wen *et al*. (2001)	AF242244
Schefflera oblongifolia Merr.	Wen *et al*. (2008)	DQ007390
Schefflera oxyphylla (Miq.) R.Vig.	Wen *et al*. (2008)	DQ007393
**Schefflera pauciflora* R.Vig.	Vietnam, Lao Cai prov., Sa Pa distr., San Sa Ho municipality, Hoang Lien National Park, Cat Cat village area, N 22°20′21″, E 103°49′12″, 1240 m, 16.12.2009. *M. S. Nuraliev 51* (MW)	JF284829
Schefflera pseudospicata Bui	Plunkett *et al*. (2005)	AY955468
Schefflera rhododendrifolia (Griff.) Frodin (listed as *S. impressa* Harms) (1)	Plunkett *et al*. (2004)	AY389051

Table 1. *Continued*

Species and specimens	Source or voucher information	Genank number
Schefflera rhododendrifolia (listed as *Schefflera impressa*) (2)	Pandey *et al*. (2004)	AY725132
Schefflera roxburghii Gamble	Plunkett *et al*. (2005)	AY955471
Schefflera pubigera (Brongn. ex Planch.) Frodin (listed as *Schefflera bengalensis* Gamble)	Wen *et al*. (2008)	AY725130
Schefflera aff. *schultzei* Harms	Plunkett *et al*. (2005)	AY955473
**Schefflera subintegra* (Craib) C. B. Shang (1)	Thailand, Chiang Mai prov., Mae Chaem distr., Doi Inthanon National Park, headquarters area, N 18°33′, E 98°28′, 2000 m, 09.02.2009. *M. S. Nuraliev*, *I. A. Savinov 5* (spirit collection at Department of Higher Plants, Moscow State University)	JF284842
**Schefflera subintegra* (2)	Thailand, Loei prov., Phu Rua distr., Phu Rua National Park, N 17°29′58″, E 101°20′28″, 1180 m, 18.01.2010. *M. S. Nuraliev*, *I. A. Savinov 58* (MW)	JF284839
**Schefflera subintegra* (3)	Thailand, Loei prov., Phu Rua distr., Phu Rua National Park, N 17°30′14″, E 101°19′36″, 1245 m, 19.01.2010. *M. S. Nuraliev*, *I. A. Savinov 59* (MW)	JF284838
**Schefflera subintegra* (4)	Vietnam, Dak Lak prov., Lak distr., Bong Krang municipality, Chu Yang Sin National Park, N 12°23′45″ E 108°20′51″, 1100 m, 11.04.2012, *M. S. Nuraliev 517* (MW)	KF134665
**Schefflera subintegra* (5)	Russia, St Petersburg, cultivated in the greenhouse # 18 of the Botanical Garden, the Komarov Botanical Institute (# 83152), 05.11.2013, *A. A. Oskolski 44-13* (MW)	JF284840
Schefflera tomentosa Harms	Plunkett *et al*. (2005)	AY955482
Schefflera trevesioides Harms	Plunkett *et al*. (2004)	AY389057
Schefflera venulosa (Wight & Arn.) Harms (1)	Pandey *et al*. (2004)	AY725126
Schefflera venulosa (2)	Russia, St Petersburg, cultivated in the greenhouse # 18 of the Botanical Garden, the Komarov Botanical Institute, 05.11.2013, *A. A. Oskolski 42-13* (MW)	JF284828
Schefflera venulosa (3)	Russia, St Petersburg, cultivated in the greenhouse # 18 of the Botanical Garden, the Komarov Botanical Institute, 05.11.2013, *A. A. Oskolski 43-13* (MW) (probably, grafted from the plant individual *A. A. Oskolski 42-13*)	JF284827
Schefflera venulosa (4)	Russia, St Petersburg, cultivated in the greenhouse # 20 of the Botanical Garden, the Komarov Botanical Institute (# 259597), 05.11.2013, *A. A. Oskolski 41-13* (MW)	JF284826
Schefflera aff. *versteegii* Harms	Plunkett *et al*. (2005)	AY955488
Schefflera yunnanensis H. L. Li	Plunkett *et al*. (2004)	AY389060
Schefflera sp. ined. *'zollingeriana'*	Wen *et al*. (2008)	AY955491
Tetrapanax papyrifer (Hook.) K.Koch	Mitchell & Wagstaff (1997)	TPU63192
Tupidanthus calyptratus Hook.f. & Thomson (= *Schefflera pueckleri* (K.Koch) Frodin) (1)	Pandey *et al*. (2004)	AY725133
Tupidanthus calyptratus (2)	Plunkett *et al*. (2004)	AY389065
Tupidanthus calyptratus (3)	Plunkett & Lowry (2001)	AF229769

Asterisks indicate sequences generated for the present study.

and additional spirit collections *no. 50* and *no. 51*]; and in southern Vietnam [*M. S. Nuraliev no. 517* (Table 1); only immature inflorescence buds]. Moreover, the mature floral buds were examined by M. S. Nuraliev and A. A. Oskolski in February 2013 in Phu Rua National Park and by M. S. Nuraliev in Chu Yang Sin National Park in April 2013. Photographs were taken with a Pentax Optio w80 digital camera from living plants in Phu Rua NP and from fixed material collected at the same place.

For light microscope observations, material from Doi Inthanon NP was used. The flowers were cross-sectioned using standard methods of paraplast embedding and serial sectioning at 15 μm thickness (Barykina *et al*., 2004). The sections were stained in picroindigocarmine and carbolic fuchsine (Axenov, 1967) and mounted in Biomount. Sections were examined and images were taken using a Axioplan microscope (Zeiss).

For scanning electron microscopy (SEM), parts of inflorescences and flowers were dehydrated in 96% ethanol followed by 100% acetone. Dehydrated material was critical-point dried using a Critical Point Dryer (Hitachi), mounted onto SEM stubs using double-sided sticky tape and sputter-coated with Pt/Pd using an IB-3 Ion Coater (Eiko) and examined using a 4DV scanning electron microscope (CamScan) at Moscow University. SEM images were treated (and some of them coloured) using CORELDRAW X5 (Corel) and PHOTOSHOP ELEMENTS (Adobe).

For phylogenetic analysis, complete sequences of nuclear ribosomal DNA internal transcribed spacer (ITS) region were generated for 26 accessions belonging to 11 species of *Schefflera s.l.*, some of which are represented by several collections. After adding GenBank data, 70 accessions representing 39 species were used for the phylogenetic analysis. GenBank accession numbers and voucher information are listed in Table 1. *Tetrapanax papyrifer* (Hook.) K.Koch and *Heteropanax fragrans* (Roxb.) Seem. were selected as outgroups based on previous higher-level phylogenetic studies (Plunkett & Lowry, 2001; Plunkett *et al*., 2004, 2005; Wen *et al*., 2008; Li & Wen, 2013).

Total DNA was isolated from leaf tissue using NucleoSpin Plant isolation kit (Macherey-Nagel) in accordance with the manufacturer's instructions. Details of polymerase chain reaction (PCR) amplifications of the ITS1-2 region and sequencing strategies used (including primer locations and characteristics) are as described by Valiejo-Roman *et al*. (2002). PCR products were purified using the DNA cleaning kit from Cytokine in accordance with the manufacturer's instructions. Direct sequencing was performed on the ABI PRISM 3100 Genetic Analyzer (Applied Biosystems), using the ABI Prism BigDye Terminator Cycle Sequencing Ready Reaction Kit for cycle sequencing reactions in accordance with the manufacturer's instructions. Forward and reverse strands of ITS samples were sequenced. Sequences were aligned in MUSCLE (Edgar, 2004) and manually adjusted using BIOEDIT (Hall, 1999).

Heuristic maximum parsimony searches were conducted in PAUP* version 4.0b8 (Swofford, 2003) using tree bisection–reconnection branch swapping and 1000 random addition replicates, with unordered (Fitch) parsimony. Bootstrap support values were calculated from 1000 replicate analyses, using a single random addition replication per bootstrap resampling, and with maximal number of saved trees per replicate set to 1000.

Bayesian inference was performed using MrBayes, version 3.2.1 (Ronquist *et al*., 2012). The GTR+Γ DNA substitution model (i.e. the general time reversible model with among site rate variation) was selected using the Akaike information criterion in MODELTEST (Posada & Crandall, 1998). Bayesian analysis was performed with four chains (one cold and three heated under default heating values) in each of two parallel runs, with each chain starting with a random tree, and then run for 25 000 000 generations; trees were sampled every 100 generations. The number of discarded generations was 30 000; from the remaining trees a majority rule consensus tree was produced.

RESULTS

ORGANOGRAPHY OF FLOWERS OF *S. SUBINTEGRA*

Each flower is situated in the axil of a bract. The pedicel bears two bracteoles at its base which are inserted at the same level close to the bract. The flower-subtending bract and bracteoles are caducous (i.e. they fall off before anthesis). Flowers are hermaphroditic, tetracyclic, with a tendency to alternation of elements in adjacent whorls, hemi-isomerous, polymerous (Figs 1–6). The size of a flower bud just before anthesis is approximately 8–12 mm. Flower shape is elliptic in the top view. The flower is usually disymmetric with median and transversal planes of symmetry, which is evident from the structure of the corolla (Figs 2A, 6A) and gynoecium (Figs 2B–D, 4, 5, 6B). The flower is wider in the transversal plane than in the median plane. Therefore, flower orientation is stable with respect to the axil of its subtending bract.

The calyx appears as an almost inconspicuous narrow circular rim below the corolla insertion (Figs 1, 2B–D). The calyx rim is continuous (i.e. the mature calyx is represented only by a short unvascularized tube with entire rim). Neither external morphology, nor anatomy allows individual sepals to be distinguished or calyx merism to be estimated.

Petals are united into a massive calyptra, which tightly encloses the androecium and gynoecium in the

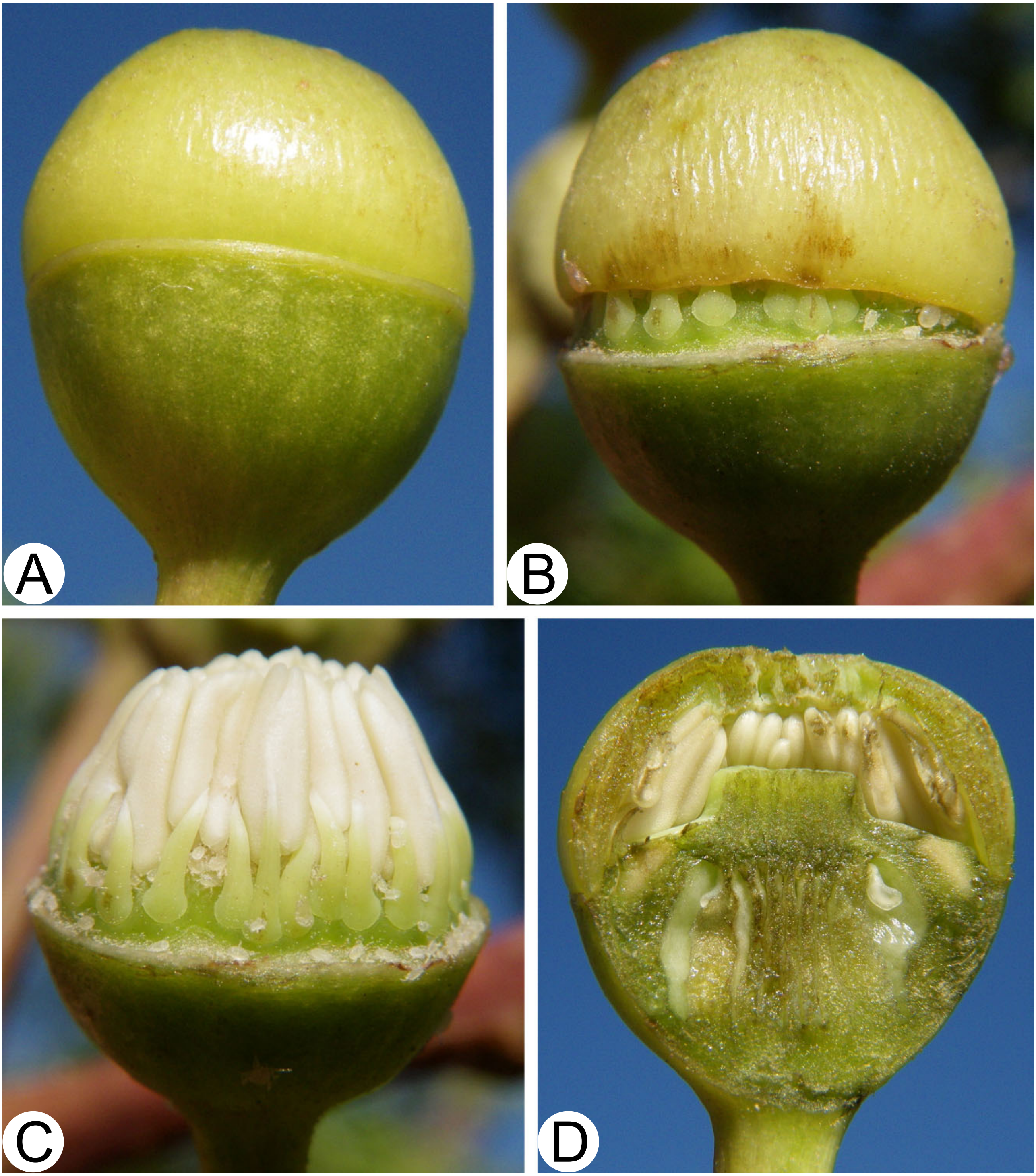

Figure 1. Flower of *Schefflera subintegra*. A, flower bud, side view. B, calyptra abscising. C, the same flower as in B with artificially opened calyptra; note the erect stamen filaments. D, longitudinal section of flower bud.

flower bud and falls off as a single unit by anthesis (Figs 1A, B, D, 2A, 3A). The mature calyptra is green or yellowish. The calyptra lacks external longitudinal ridges and any other traits of individual petals. No borders between petals were also distinguished on the cross-sections of the calyptra (Fig. 6A). The rim of the corolla tube is curved inwards, and two transversal opposite parts of the tube are fused postgenitally with

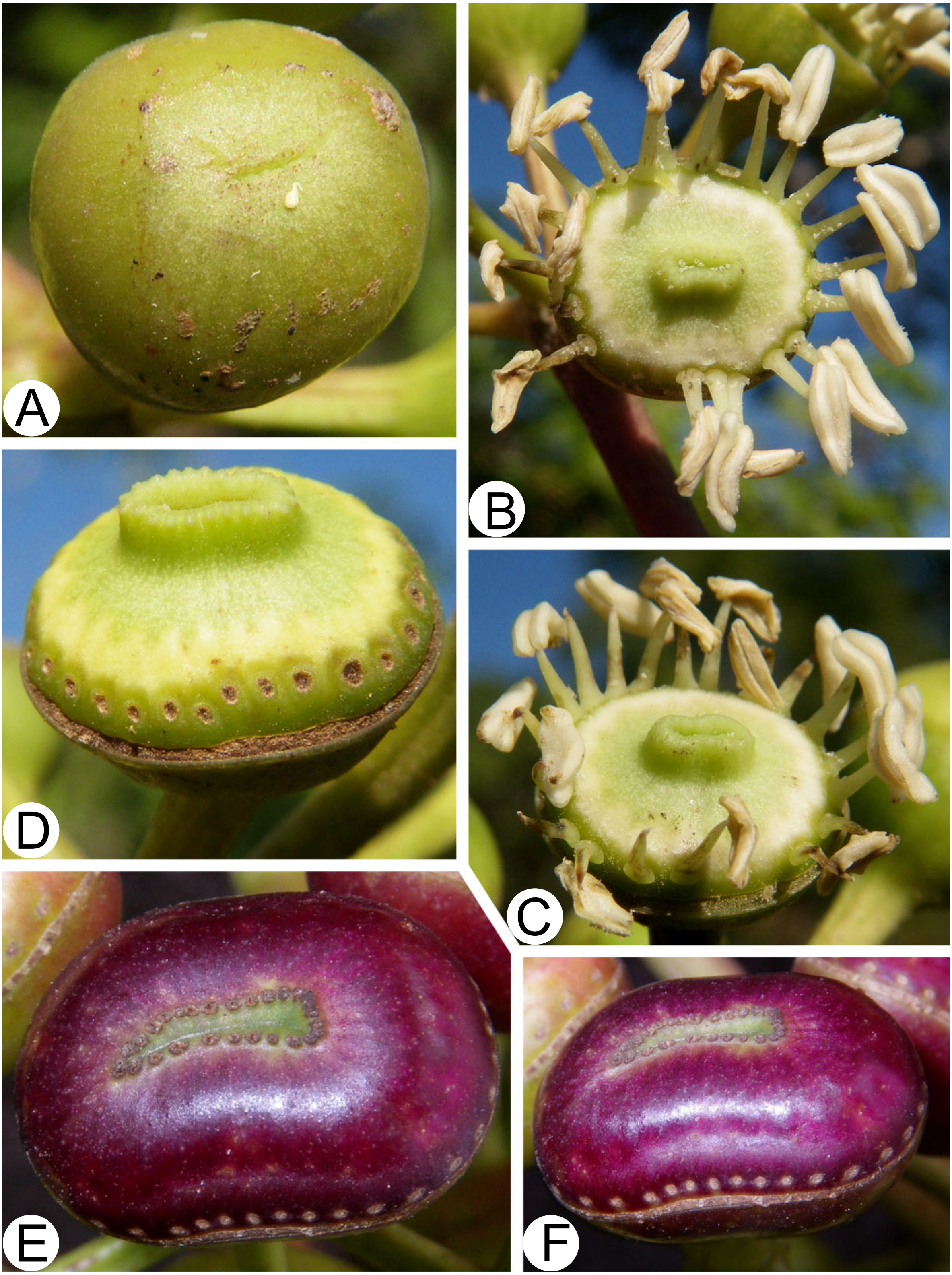

Figure 2. Flower of *Schefflera subintegra*. A, flower bud, top view, showing calyptra with trace of postgenital fusion in the centre. B, open flower with two stamens abscised, top view. C, open flower with two stamens abscised, side view. D, immature fruit; note circular stamen scars. E, F, ripe fruit; note the style no longer conspicuous and well-pronounced stigmas.

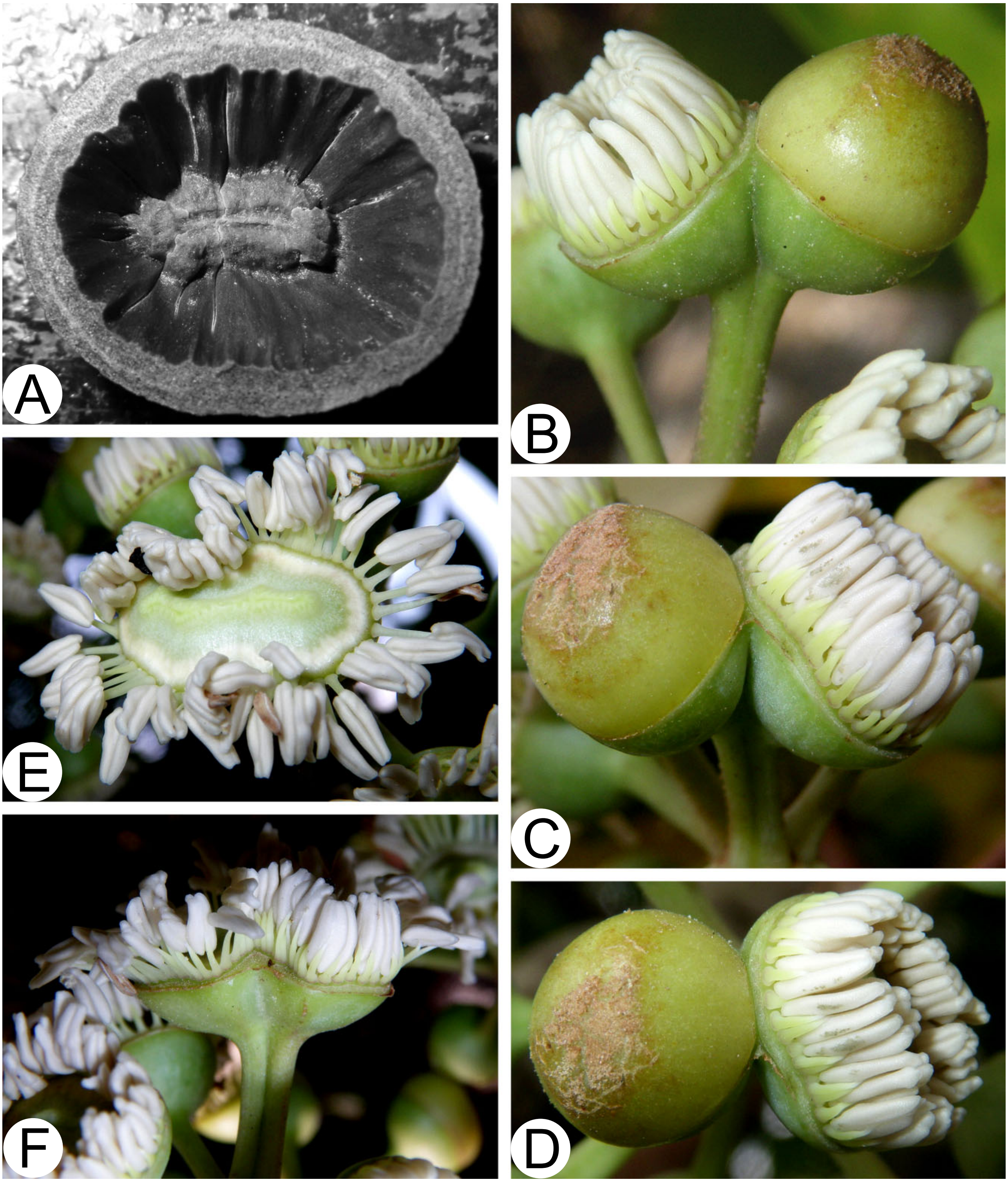

Figure 3. Flower of *Schefflera subintegra*. A, detached calyptra, view from below (from fixed material); note the imprint of the style in its centre. B–D, double flower with independent floral whorls. E, F, double flower with common floral whorls.

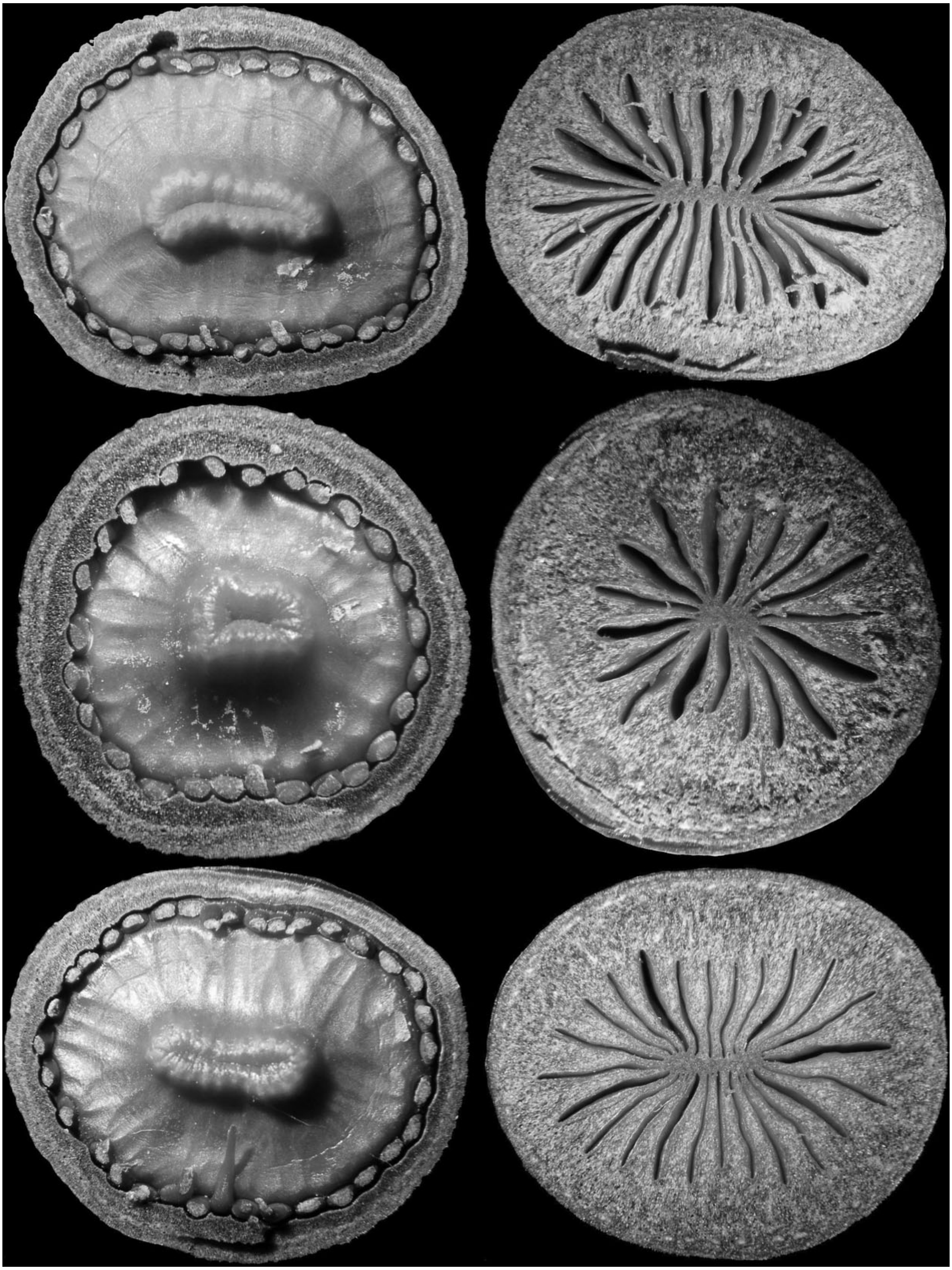

Figure 4. Variation of floral merism and style shape in *Schefflera subintegra* (from fixed material). Left column, flower top view with calyptra and stamens removed showing the filament bases and upper part of the ovary. Right column, cross-section of the same flower as in the left column at the level of synascidiate zone of the gynoecium, showing the ovary locules.

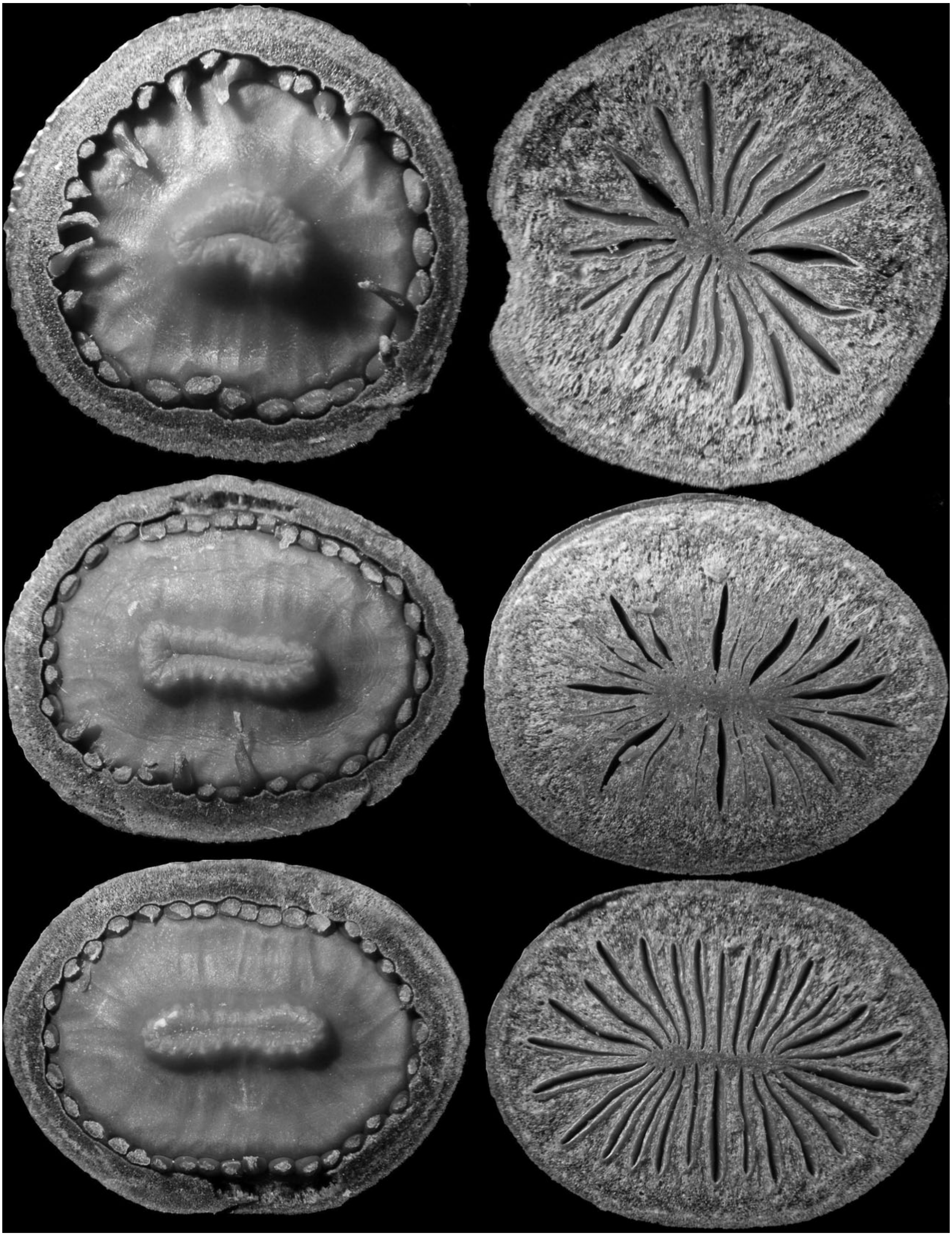

Figure 5. Variation of floral merism and style shape in *Schefflera subintegra* (continued from Fig. 4).

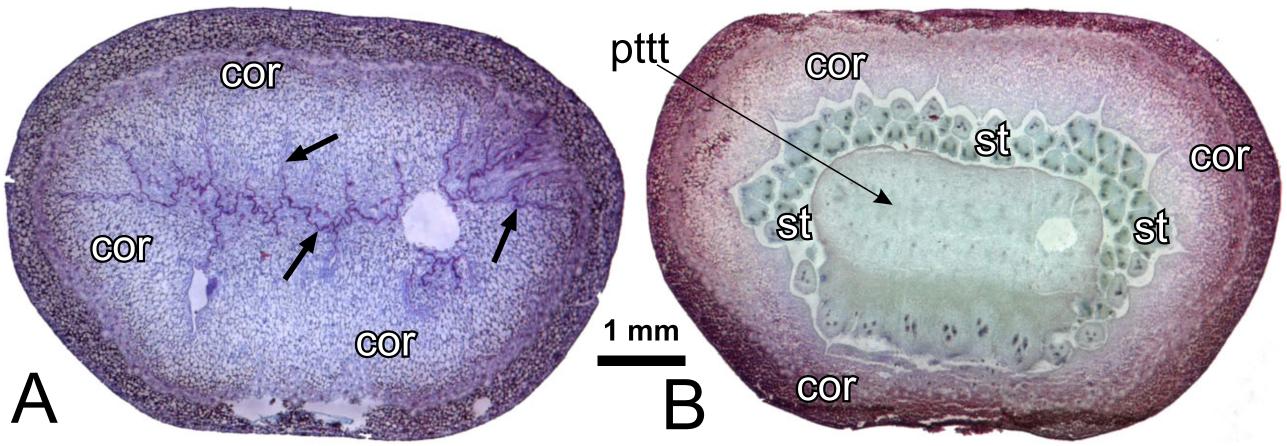

Figure 6. Cross-sections of immature flower bud of *Schefflera subintegra* at the final stages of the development. A, upper level of the calyptra, showing sutures of fusing of the corolla folds (arrows). B, level of the style base, slightly oblique with the lower part being below the attachment of the floral elements; note the elongated compitum and continuous structure of the calyptra. Cor, corolla; st, stamen; pttt, pollen tube transmitting tissue.

their morphologically abaxial surfaces. The postgenital closure of the corolla tube is marked by a short transversal suture at the calyptra apex (Fig. 2A) and by a pronounced fusion line at the centre of cross-sections of the upper part of the calyptra (Fig. 6A). This line is branched as a result of the presence of folds at the fused corolla edges, which also fuse with each other laterally. Because the folds are rather short and occupy different levels, their number is not clear, although there are most probably not more than 20. Some of the folds are rather deep, whereas others are shallow. The folds on opposite sides of the calyptra alternate with each other along the line of postgenital closure. The morphologically adaxial surface of the calyptra is irregularly ridged (Fig. 3A) because it reflects the shape of the stamens and upper part of the gynoecium, which are adpressed to the calyptra at some stages of development (the gynoecium before the intercalary corolla growth and the stamens until flower opening).

In the flowers examined, the androecium consists of one whorl of 19–43 stamens and the gynoecium is composed of a whorl of 15–33 united carpels (Figs 4, 5). Within a flower, stamens are always more numerous than carpels, with the difference varying from a single element up to 1.7 times. The following examples of androecium and gynoecium merism are observed in our material: $A_{19}G_{15}$, $A_{20}G_{18}$, $A_{21}G_{17}$, $A_{22}G_{18}$, $A_{22}G_{20}$, $A_{23}G_{18}$, $A_{24}G_{23}$, $A_{29}G_{27}$ (all in a specimen from Doi Inthanon NP), $A_{26}G_{18}$, $A_{27}G_{22}$, $A_{28}G_{19}$, $A_{28}G_{23}$, $A_{34}G_{25}$, $A_{35}G_{27}$, $A_{37}G_{24}$, $A_{37}G_{25}$, $A_{38}G_{22}$, $A_{39}G_{33}$, $A_{42}G_{29}$ (all in specimens from Phu Rua NP), $A_{32}G_{?}$, $A_{33}G_{?}$, $A_{35}G_{25}$, $A_{35}G_{29}$, $A_{36}G_{27}$ $A_{37}G_{29}$, $A_{43}G_{31}$ (all in a specimen from Chu Yang Sin NP). Filaments are flattened with considerably dilated base, light green, straight in the flower bud (Fig. 1C). The anthers are yellowish white and represent the only bright parts of the anthetic flower (Fig. 2B, C). Because the anthetic stamens spread away from the stigmas resembling petals of a ‘typical’ eudicot flower, they appear to be a visual attractant for pollinators. After abscission of the stamens, distinctive circular to oval scars remain at the base of ovary disk (Fig. 2D). The rare occurrence of teratological structures resembling a stamen filament curved towards the gynoecium disk and completely fused to its surface is documented.

The ovary is semi-inferior (Fig. 1D). Its superior part is pale green, whereas the inferior ovary wall is dark green outside. The superior part of the ovary is several times shorter than the inferior part and represented by a flat disk. There is a short but distinct style approximately 1–2 mm high (Figs 1D, 2B,C). The style becomes somewhat higher during fruit maturation (Fig. 2D). The style is slightly concave as a result of incomplete postgenital intercarpellary fusion of the upper carpel margins. The style is narrowly elliptic in outline and follows the overall flower shape in its orientation. These peculiarities of flower and style symmetry are related to the gynoecium structure. The gynoecium is syncarpous, with a long synascidiate and a short symplicate zone. The number of locules in the synascidiate zone corresponds to the number of carpels, and the ventral parts of the carpels meet each other in the flower centre. Morphologically, the carpels are arranged in a single whorl, although the whorl is distorted so that it is rather elliptic (elongated in the transversal plane of a flower) than circular (Figs 2B, 4, 5, 6B). Therefore, the carpels do not contact each other in one and the same place in the floral centre but the area of their ventral contact forms a kind of line on cross-section of a flower. This line follows the direction of elliptic distortion of the carpel whorl. Each carpel contacts two neighbouring carpels on the same side of the whorl and usually two carpels of the opposite side. This feature of gynoecium structure can be inferred from the arrangement of stigmas in the top view of a flower and from the relative position of ovary locules at cross-sections. While in many flowers the carpels lie along a simple plane, the line of carpel arrangement viewed from the top is unbranched and the style shape is elliptic, in some other flowers, the carpels are arranged in a more complex shape. In the latter, the line is branched once or twice and the style is correspondingly lobed in the outline, which disturbs the overall disymmetry of the flower (Figs 4, 5).

The cross zone of the carpels is situated slightly above the border between inferior and superior ovary parts (Fig. 1D). The locules do not extend above the cross zone as a result of complete postgenital fusion of the ventral carpel margins within the symplicate zone. Each locule possesses a single pendent fertile ovule; no evidence of sterile ovules was found. Stigmas are carinal, sessile, slightly decurrent, glabrous, externally better recognizable in fruit than in flower (Fig. 2E, F). The ovary wall is rather thick and smooth outside. The strands of pollen tube transmitting tissue start from the stigmas and approach each other slightly above the cross zone to merge into an internal compitum (Fig. 6B). The compitum is narrowly elliptic or zigzag-shaped corresponding to the manner of carpel arrangement. Each locule receives a strand of the pollen tube transmitting tissue from the compitum.

The ripe fruit of *S. subintegra* is broadly elliptic in outline, approximately 2 cm wide and dark purple (Fig. 2E, F). It bears clearly visible stigmas and scars of calyptra and stamens. The fruit differs significantly from the flower in its shape as a result of the considerably enlarged upper part of the ovary, which becomes equal to the lower part in height. This enlargement is accompanied by arching of the disk, which leads to complete disappearance of the style. Neither flowers, nor fruit have lenticels on the outer surface of the ovary wall or anywhere else.

Double flowers of *S. subintegra* are rarely found in the same inflorescences with normal flowers (Fig. 3B–F). These structures look like two flowers fused laterally to various degrees. In some cases, they possess a common broad pedicel with longitudinal groove and marginally united ovaries; the carpels are arranged in two independent whorls and the calyces, calyptras, and androecia are separated and do not differ from those of two normal flowers (Fig. 3B–D). In other cases, the fusion is more pronounced and affects all floral whorls; such double flowers possess a single common calyx, corolla, androecium, and gynoecium, and differ from a single normal flower only in increased size and number of floral elements and in grooves on the pedicel, which continue into grooves on the opposite sides of the common ovary (Fig. 3E, F). Moreover, slightly increased size and grooved pedicels are sometimes observed in flowers that appear normal in other respects, which smoothes the border between normal and double flowers.

ORGANOGENESIS OF FLOWERS OF *S. SUBINTEGRA*

Material from three populations is used for developmental studies. Figures 7–14 illustrate plants from Chu Yang Sin NP, from early to late floral developmental stages; Figures 15–19 show plants from Phu Rua NP, from middle to late developmental stages; and Figures 20 and 21 are based on plants from Doi Inthanon NP, final stages.

Each flower is initiated in the axil of the flower-subtending bract and possesses two floral prophylls (bracteoles) in transversal positions (Figs 7A, 9A, E, 15I). The flower-subtending bract and the bracteoles are covered with multicellular tree-shaped hairs, rather densely abaxially and marginally and less densely adaxially.

The flower is polysymmetric and circular in the top view at the earliest stages of the development (Fig. 7A–C). By the time the corolla tube completely covers the undifferentiated floral centre (when the flower is approximately 0.4–0.5 mm in diameter), the flower shape changes dramatically and becomes distinctly elliptic in outline in the top view (Fig. 8A–D, 9A–C, E). The widest side of the flower lies in the transversal plane (with respect to the position of the flower-subtending bract), and the two bracteoles cover the most distant sides of the developing flower (Figs 8A–C, 9A–C, E). In some flowers, a lateral groove develops at the broader (probably abaxial) side. This groove is not visible in mature flowers. Floral whorls appear in an acropetal sequence.

The calyx is initiated as a narrow continuous meristematic ring (tube), which elongates for some time. Similarly, the corolla appears as a tube without free petal lobes (Figs 7, 8). The corolla tube lies parallel to the flat floral meristem instead of standing upright since the earliest stages.

At the stage of stamen initiation, the flower is approximately 1 mm in its widest (transversal) diameter and approximately 0.5 mm in the narrowest (median) diameter (Figs 10A–C, 15A, B, F). At this stage, the calyx is represented by a thin but well pronounced tube approximately 50 μm high (i.e. several cell layers), with no evidence of free parts of sepals. The corolla tube is extremely thick and strongly bent towards the flower centre so that its rim

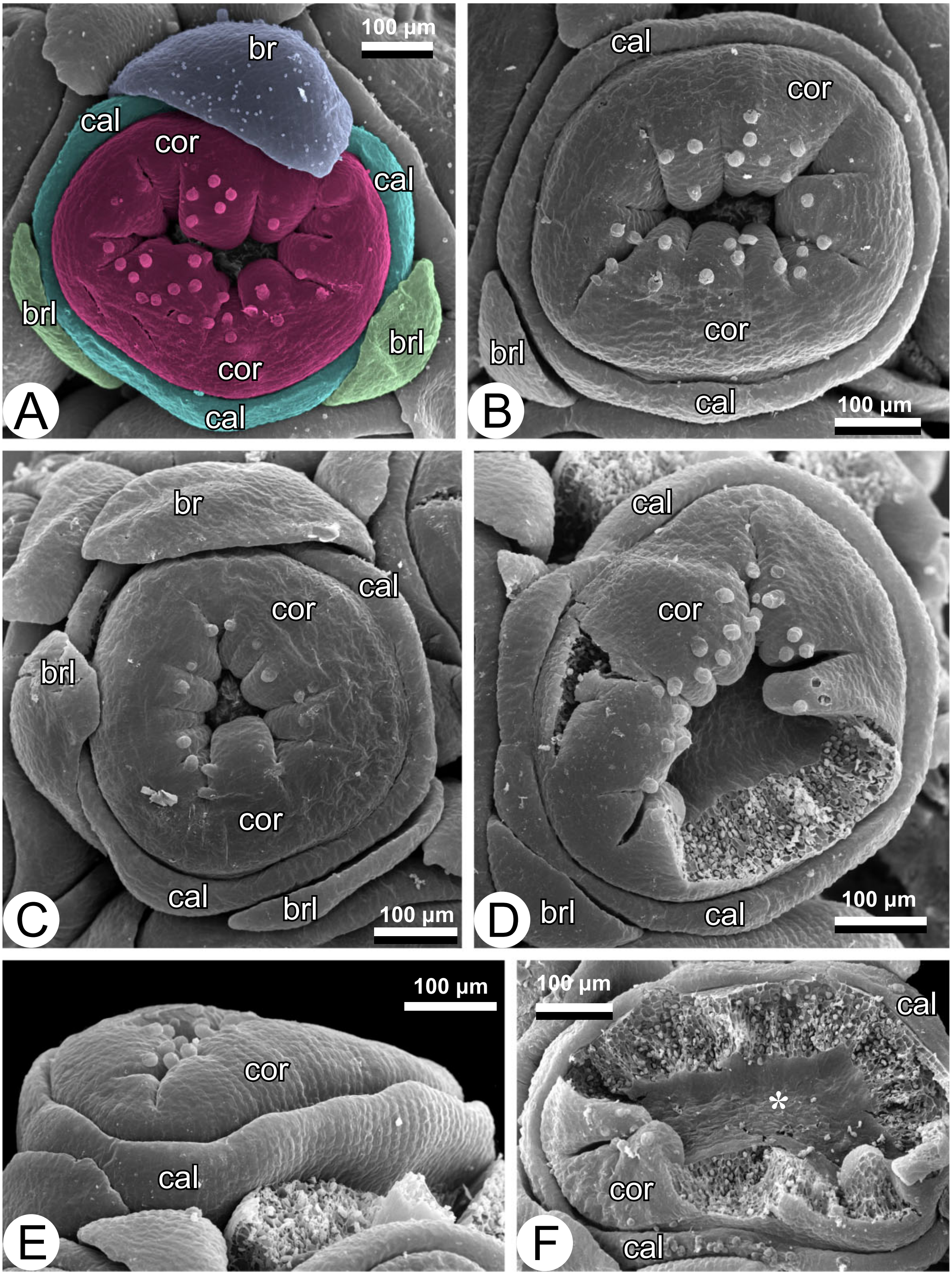

Figure 7. Floral morphogenesis of *Schefflera subintegra* from Chu Yang Sin at the stages before closure of corolla tube; note developing hairs around the corolla orifice. A–C, top view of the flower; note the flower polysymmetry and the irregularly folded corolla tube. D, flower top view, corolla partly removed. E, side view of the flower. F, flower top view with corolla almost completely removed showing flat undifferentiated zone inside the corolla tube (asterisk). Br, flower-subtending bract; brl, bracteole; cal, calyx; cor, corolla.

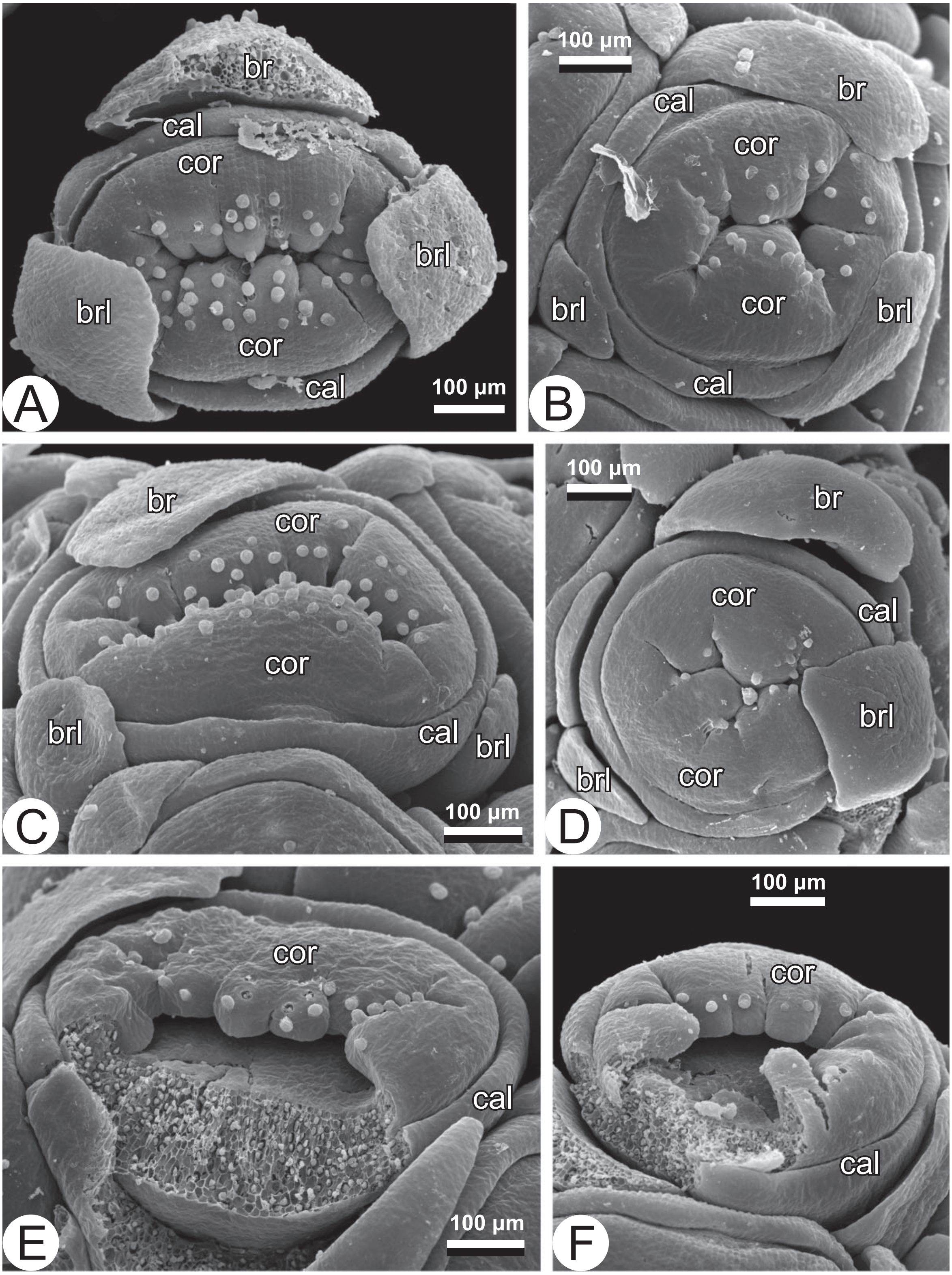

Figure 8. Floral morphogenesis of *Schefflera subintegra* from Chu Yang Sin at the stages of corolla tube closure. A, B, D, top view of the flower, showing the shape of corolla suture. C, side view of the flower. E, F, side view of the flower with calyx and corolla partly removed showing the folds of corolla tube from the inside lying parallel to the surface of undifferentiated meristem. Br, flower-subtending bract; brl, bracteole; cal, calyx; cor, corolla.

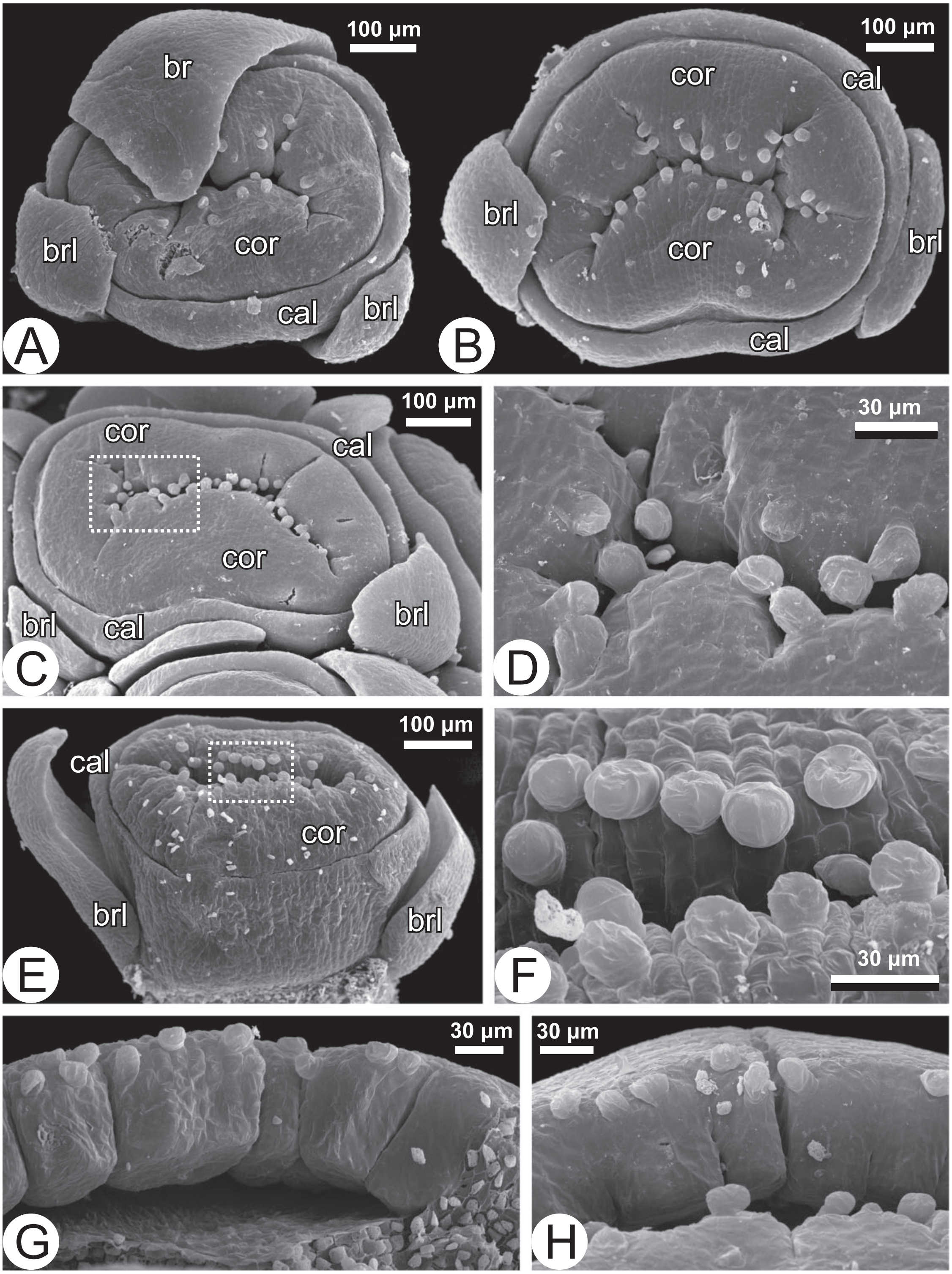

Figure 9. Floral morphogenesis of *Schefflera subintegra* from Chu Yang Sin; details of corolla structure at the stage of its closure. A, B, top view of the flower. C, side view of the flower. D, close-up of the region contoured in (C) showing the unsealed corolla suture surrounded by developing hairs. E, flower side view showing two transversal bracteoles. F, close-up of the region contoured in (E) showing the developing hairs along the corolla suture. G, inside view of a transversal half of the corolla tube showing the folds and hairs along their upper margin. H, side view of the corolla with one of its halves slightly artificially elevated. Br, flower-subtending bract; brl, bracteole; cal, calyx; cor, corolla.

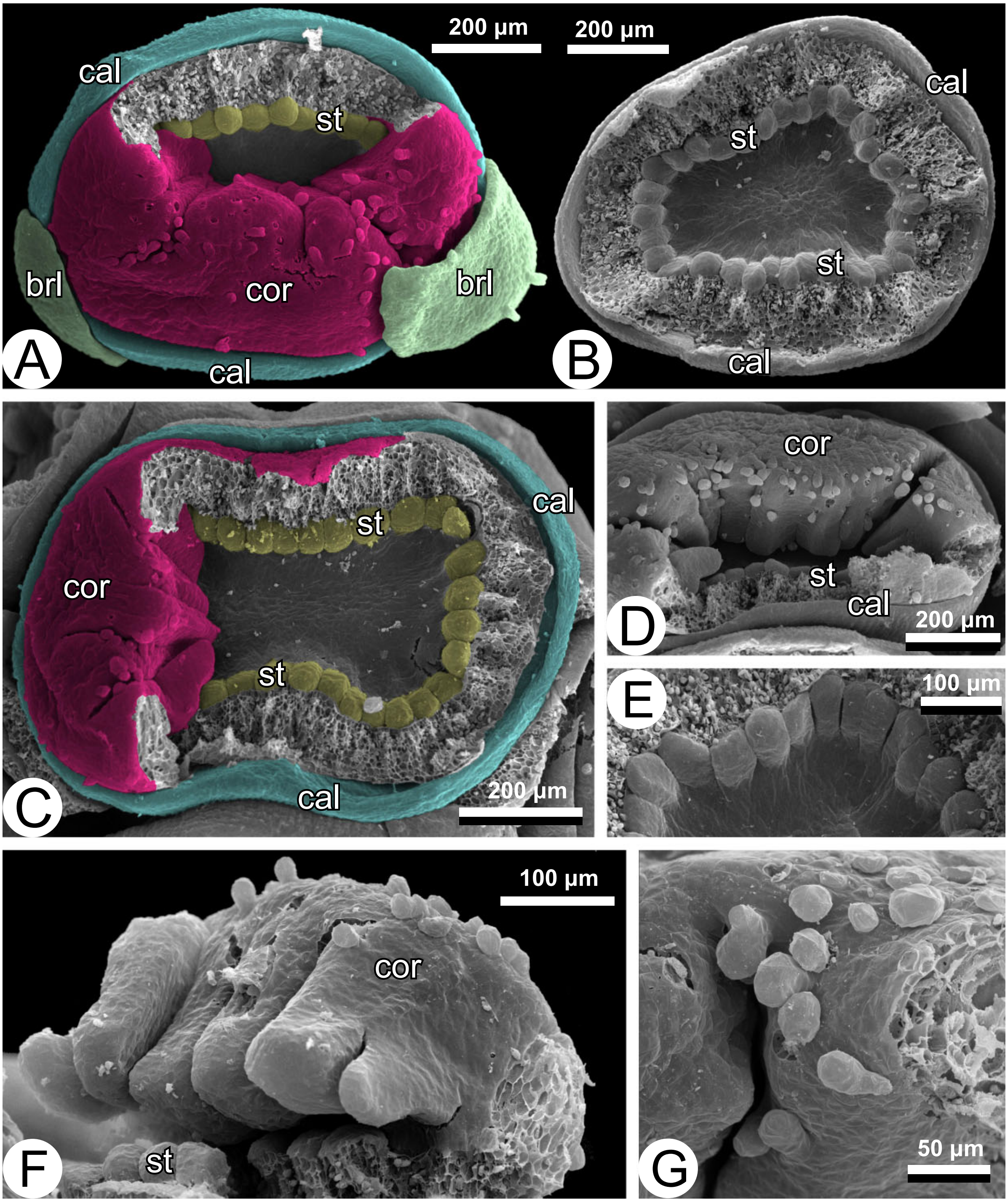

Figure 10. Floral morphogenesis of *Schefflera subintegra* from Chu Yang Sin at early stamen development. A, flower top view with corolla partly removed. B, flower top view with corolla fully removed. C, flower top view with most of corolla removed showing rim of corolla curved inwards and touching the undifferentiated flower meristem. D, flower side view with corolla partly removed showing the development of special hairs along the suture of corolla closure. E, top view of young stamens crowded into a single whorl. F, part of corolla tube artificially bent outwards from the stamens showing the lateral surface of the folds which will fuse with the opposite corolla side and their morphologically apical margin facing the area of future gynoecium arising. G, close-up of the inner margin of corolla suture with hairs developing along the border of closure area as well as below this level, at the very surface of future closure. Brl, bracteole; cal, calyx; cor, corolla; st, stamen.

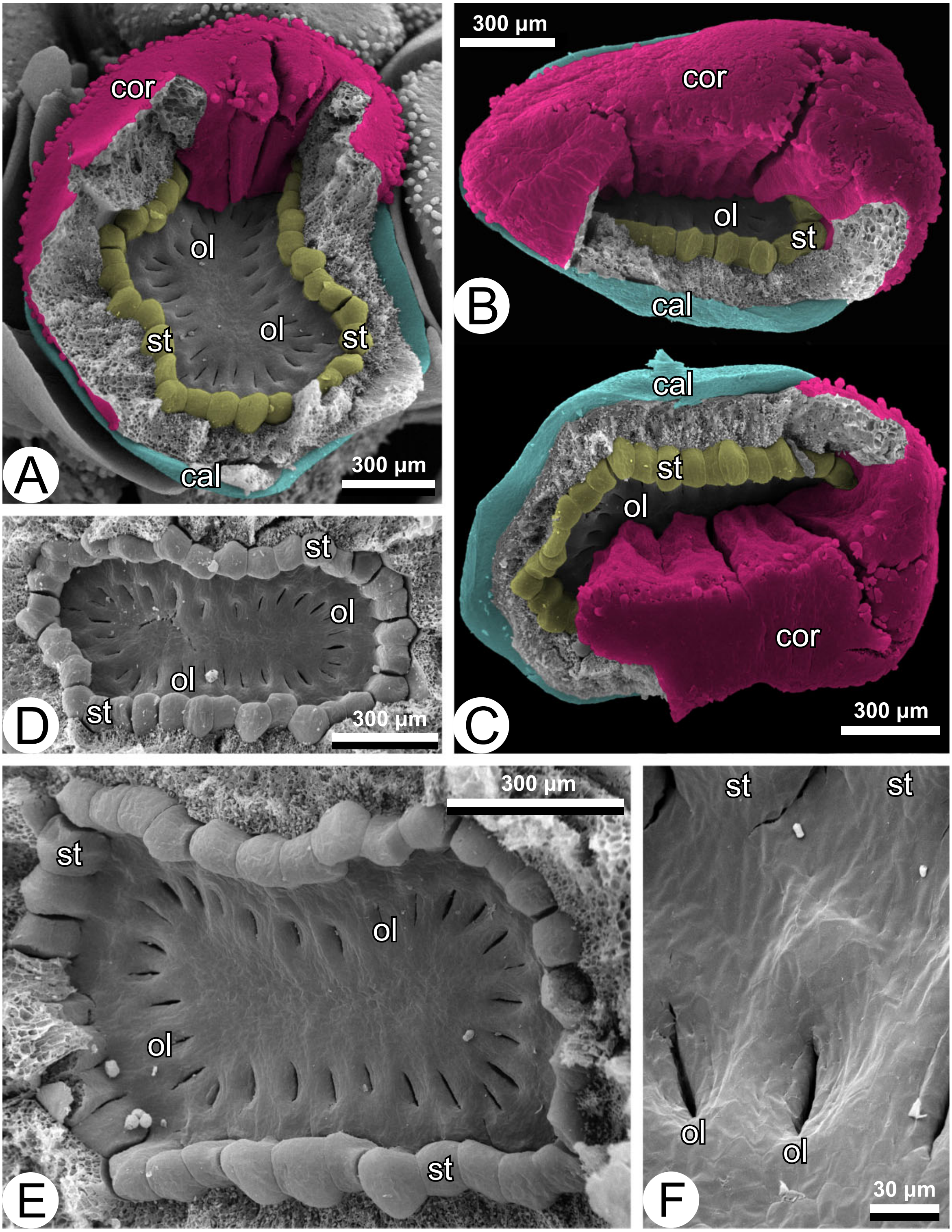

Figure 11. Floral morphogenesis of *Schefflera subintegra* from Chu Yang Sin at early development of synascidiate zone of the gynoecium. A, flower with most of corolla removed; note the apical corolla margin touching the gynoecium and numerous hairs arising at the base of the corolla outer surface. B, C, flower top view with corolla partly removed. D, E, androecium and gynoecium, top view; note the narrowly elliptic shape of the gynoecium whorl. F, close-up of developing carpel with well pronounced ascidiate part (the locule) and slightly rised plicate part. Cal, calyx; cor, corolla; ol, ovarian locule; st, stamen.

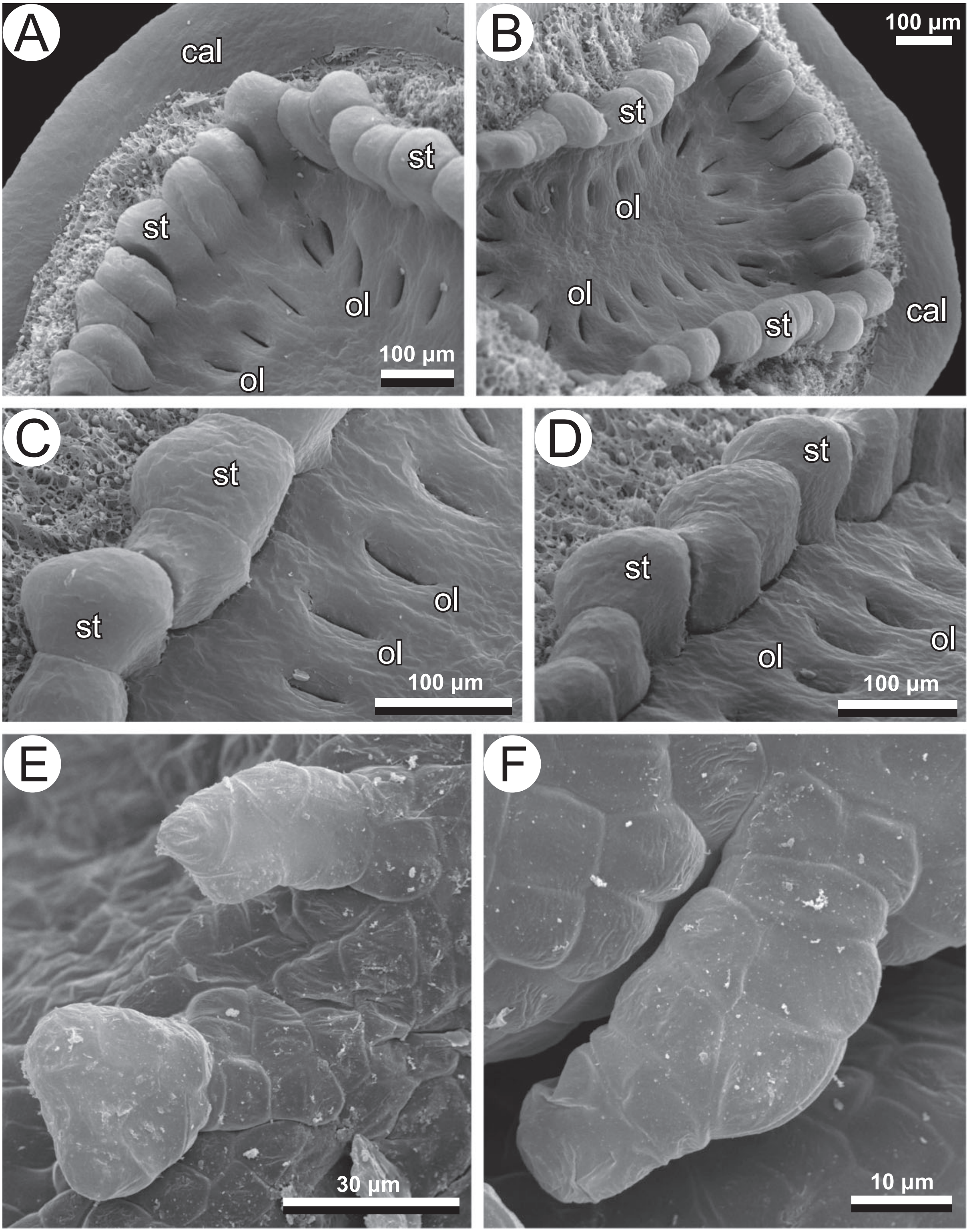

Figure 12. Details of flower structure of *Schefflera subintegra* from Chu Yang Sin at the stages of development of synascidiate zone of gynoecium. A, B, part of flower with corolla removed; note the absence of strict alternation of androecium and gynoecium whorls. C, close-up of stamens and locules, top view. D, close-up of stamens and locules, side view; note the shape of young stamens flattened by each other from the lateral sides. E, F, close-up of the special hairs involved into the corolla closure. Cal, calyx; ol, ovarian locule; st, stamen.

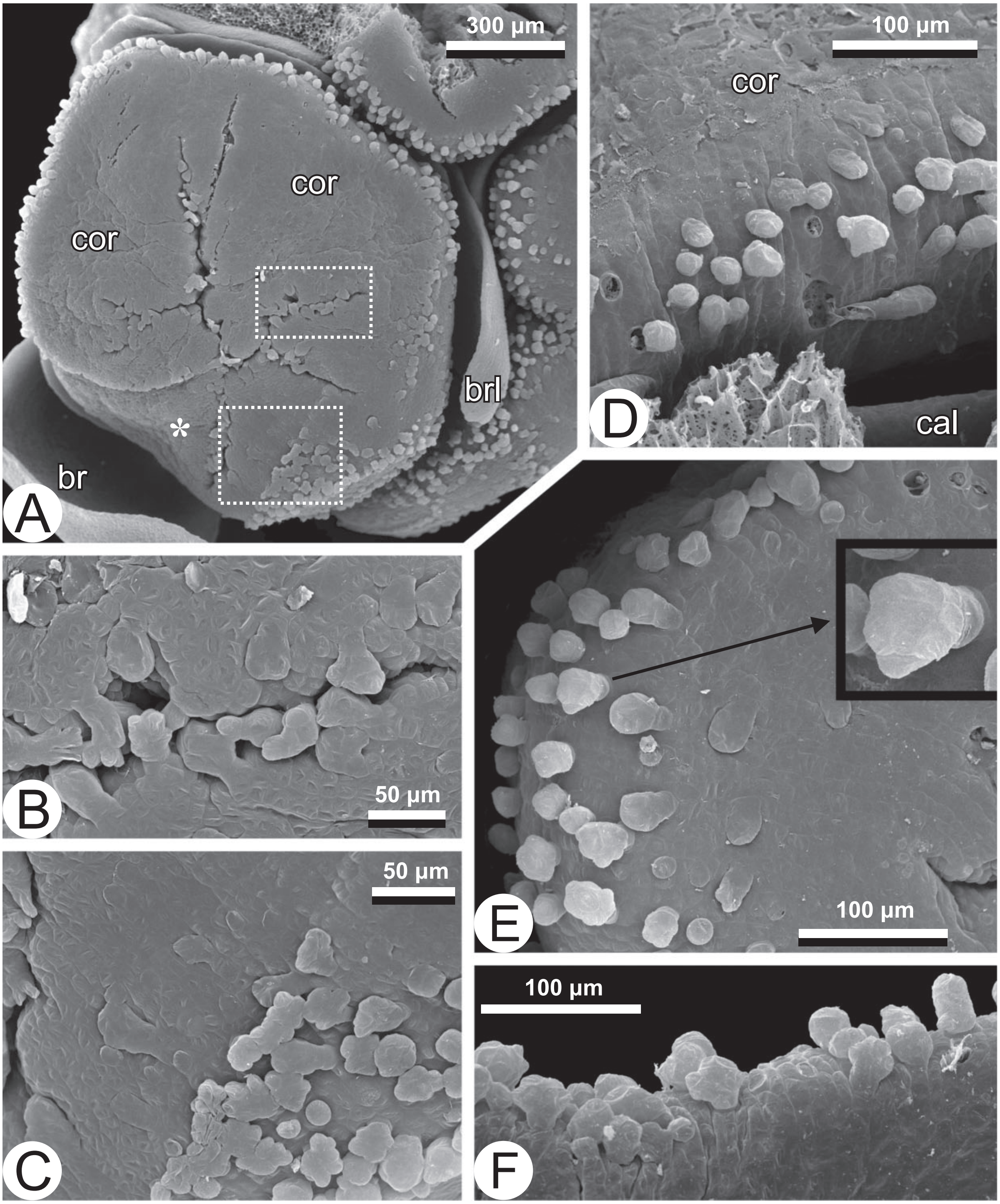

Figure 13. Flowers of *Schefflera subintegra* at the same stages as in Fig. 12, developing corolla indumentum. A, flower top view with a bract artificially bent outwards showing the area of its pressure to the corolla (asterisk); note the special hairs along the corolla suture as well as numerous hairs at the base of its outer surface. B, close-up of the upper region contoured in (A) showing special corolla hairs forming zipper-like structure over the corolla suture, which are slightly pressed by other parts of the inflorescence bud. C, close-up of the lower region contoured in (A) showing the immature stellate hairs which development is arrested at the area of bract pressure. D, side view of the corolla showing development of stellate hairs. E, F, top view of corolla margin with developing stellate hairs. Br, flower-subtending bract; brl, bracteole; cal, calyx; cor, corolla.

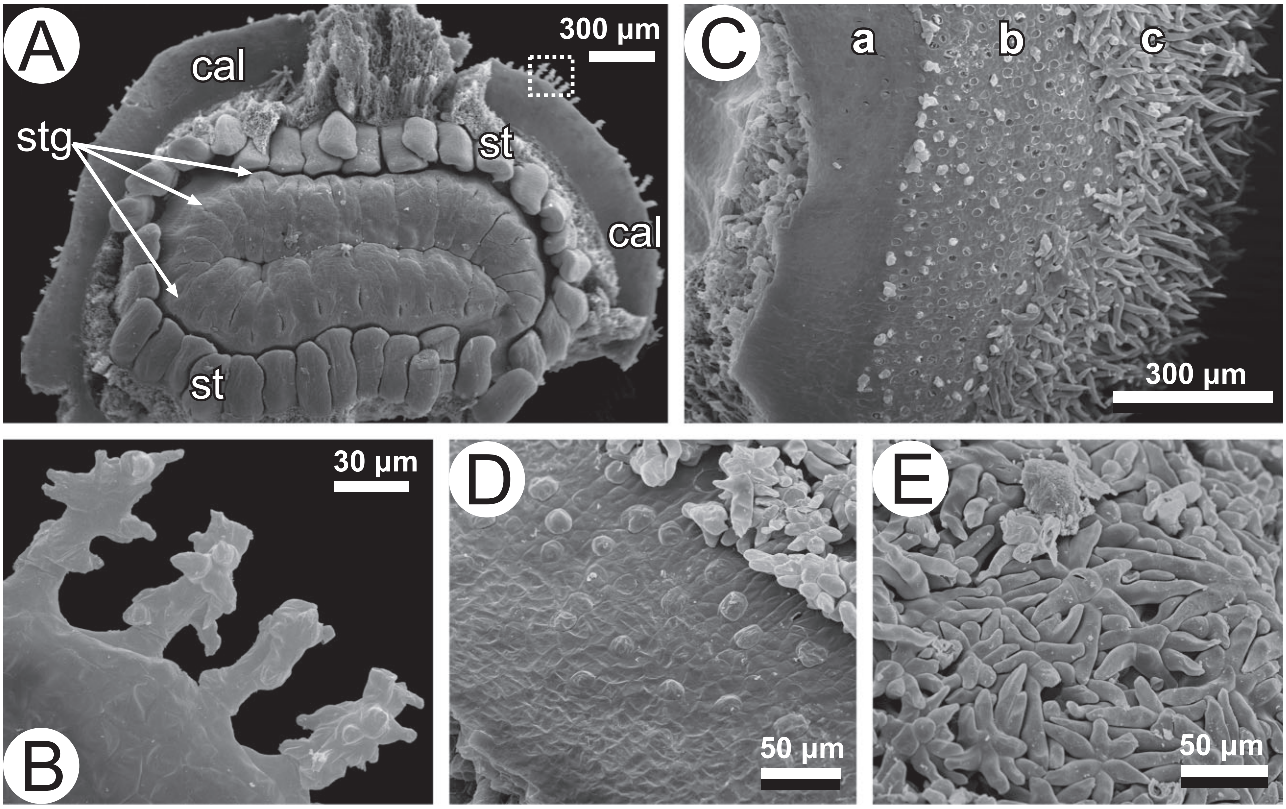

Figure 14. Final stages of flower development of *Schefflera subintegra* from Chu Yang Sin. A, flower top view, corolla removed; note the disymmetric mode of carpel arrangement. B, close-up of tree-shaped calyx hairs from the flower in (A). C, part of calyptra, view from below; note the basalmost region adjacent to the area of calyptra detachment shaped by the pressure of calyx (a), which looks glabrous, the middle region undergone the pressure of bract or bracteole (b) with underdeveloped hairs and the distal region free of pressure (c) covered with dense indumentum of stellate hairs. D, close-up of the calyptra surface equivalent to region (a) in (C) showing the hairs for which development is severely arrested by the calyx pressure. E, close-up of the calyptra surface equivalent to region (c) in (C) showing the structure of normally developed stellate hairs. Cal, calyx; st, stamen; stg, stigma.

and adaxial surface touch the undifferentiated floral central part (Fig. 10A, C, D, F). The opposite parts of the corolla tube meet each other above the floral centre and become contiguous with the morphologically abaxial surfaces. At this and further stages, the corolla tube grows mainly by extensive thickening (and probably also in intercalary extension), which results in its height becoming equal to that of the rest of the flower, and also in the abaxial corolla surface becoming much wider than the adaxial surface. No free parts of petals are visible at these developmental stages; however, the corolla tube is folded along its inner side (Figs 10F, 15G, H, 17A, E, 18B–D). Commonly, the corolla tube has ten to 12 irregularly arranged folds, which are more densely spaced on the lateral sides (i.e. the sides closest to the bracteoles), where the tube viewed from the top possesses the lowest radius of curvature. At middle stages of flower development, the transversal opposite sides of the corolla tube fuse postgenitally with each other and completely enclose the androecium and gynoecium. This process is followed by lateral postgenital fusion of neighbouring corolla folds. Because the tube is curved inwards, its postgenital closure occurs by fusion between adjacent abaxial surfaces. At the site of postgenital fusion, cell walls of the abaxial corolla epidermis develop a specific ribbed sculpture (Figs 19F, 20C–E). The ribs and grooves on the adjacent epidermal surfaces are complementary to each other, resulting in a tight adnation. Short multicellular weakly branched hairs, each consisting of a few crowded cells, develop along the outer edge of the area of the corolla closure (Figs 9D–H, 10F, G, 12E, F, 13A, B, 17F, 18). The hairs of the opposite corolla sides touch each other and form a zipper-like structure to complete the closure. During later stages of development, numerous stellate hairs arise at the outer surface of the corolla (i.e. the abaxial surface

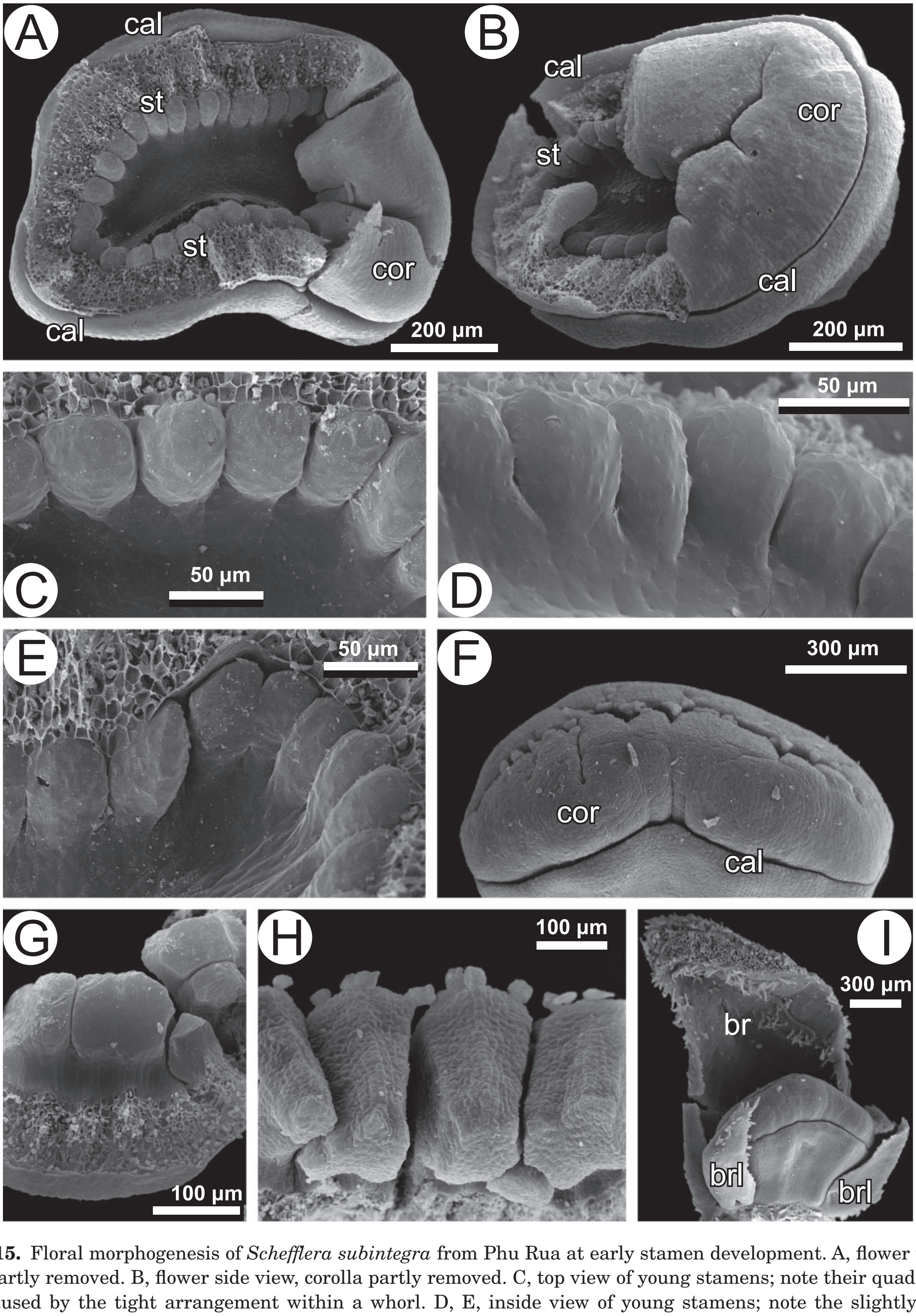

Figure 15. Floral morphogenesis of *Schefflera subintegra* from Phu Rua at early stamen development. A, flower top view, corolla partly removed. B, flower side view, corolla partly removed. C, top view of young stamens; note their quadrangular shape caused by the tight arrangement within a whorl. D, E, inside view of young stamens; note the slightly concave receptacle. F, perianth side view. G, detached part of the corolla viewed from below; note the folds with their apices facing the flower meristem. H, part of the corolla at later stage than (G) artificially bent outwards and viewed from the inside showing the folds with special hairs at their upper margin and their lower morphologically apical margin facing the flower meristem. I, adaxial side view of a flower with a bract and two transversal bracteoles. Br, flower-subtending bract; brl, bracteole; cal, calyx; cor, corolla; st, stamen.

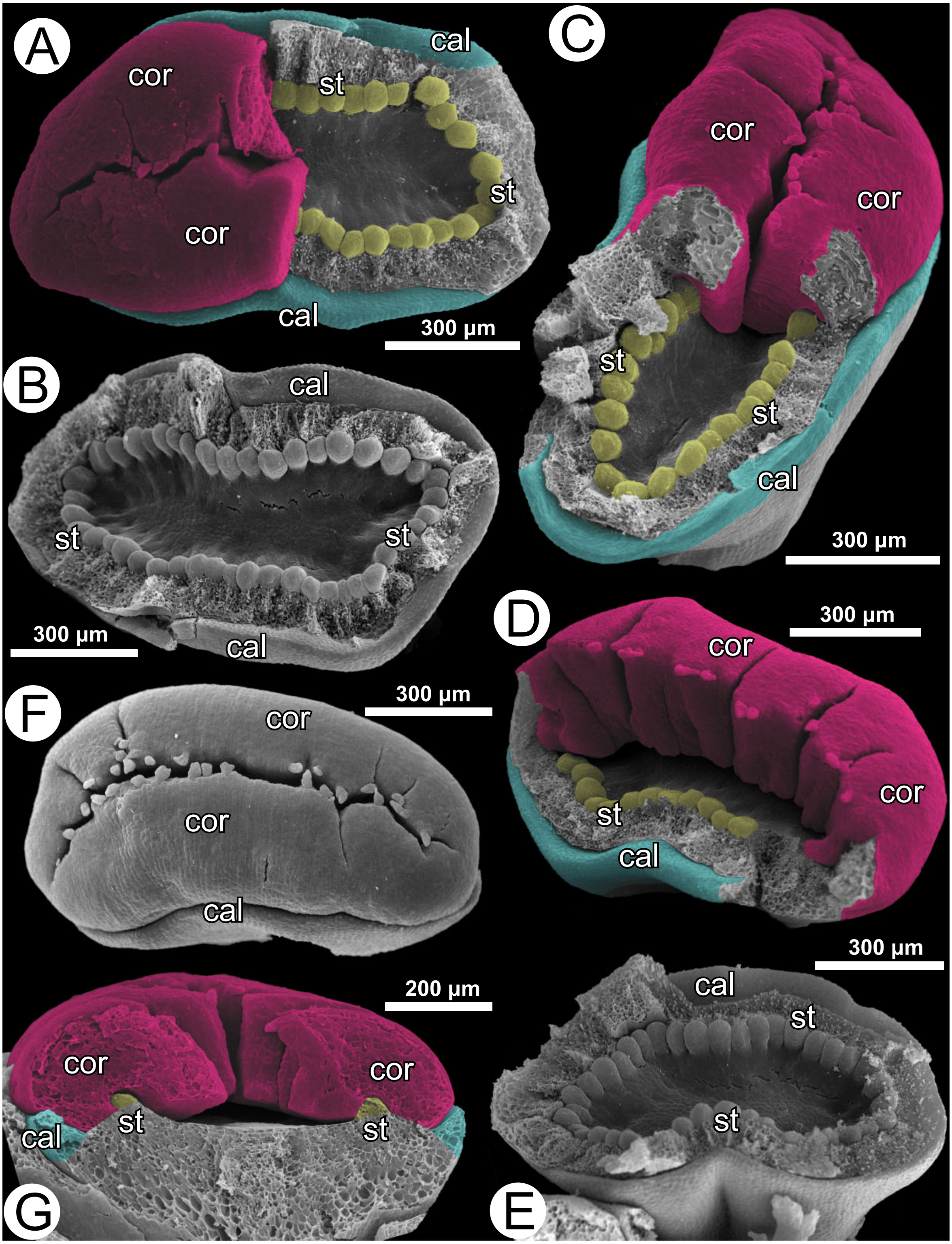

Figure 16. Floral morphogenesis of *Schefflera subintegra* from Phu Rua at the very beginning of gynoecium development. A, flower top view, corolla partly removed. B, flower top view, corolla removed; note the folded surface inside the androecium indicating arising ovary locules. C, flower, with corolla partly removed; note slightly concave receptacle. D, flower side view, corolla partly removed. E, flower side view, corolla removed. F, flower top view, showing the perianth. G, longitudinal section of flower. Cal, calyx; cor, corolla; st, stamen.

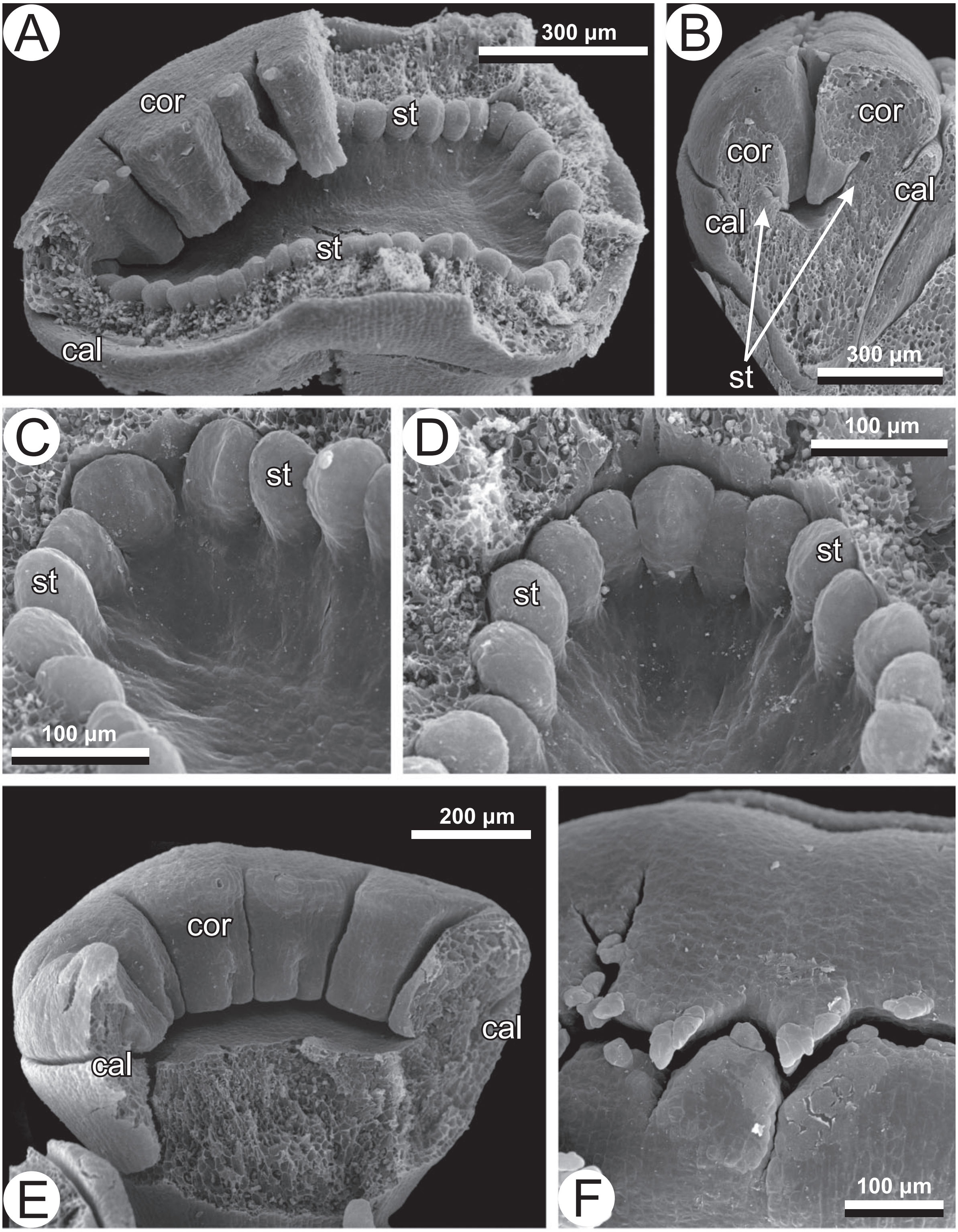

Figure 17. Details of flower structure of *Schefflera subintegra* from Phu Rua at the beginning of gynoecium development. A, flower side view, corolla partly removed. B, longitudinal section of flower; note the concave shape of undifferentiated meristem. C, D, part of a flower with corolla removed, inside view; note the arising ovary locules. E, flower longitudinal section showing corolla folds. F, part of corolla, top view, showing the manner of corolla closure and special hairs along the suture. Cal, calyx; cor, corolla; st, stamen.

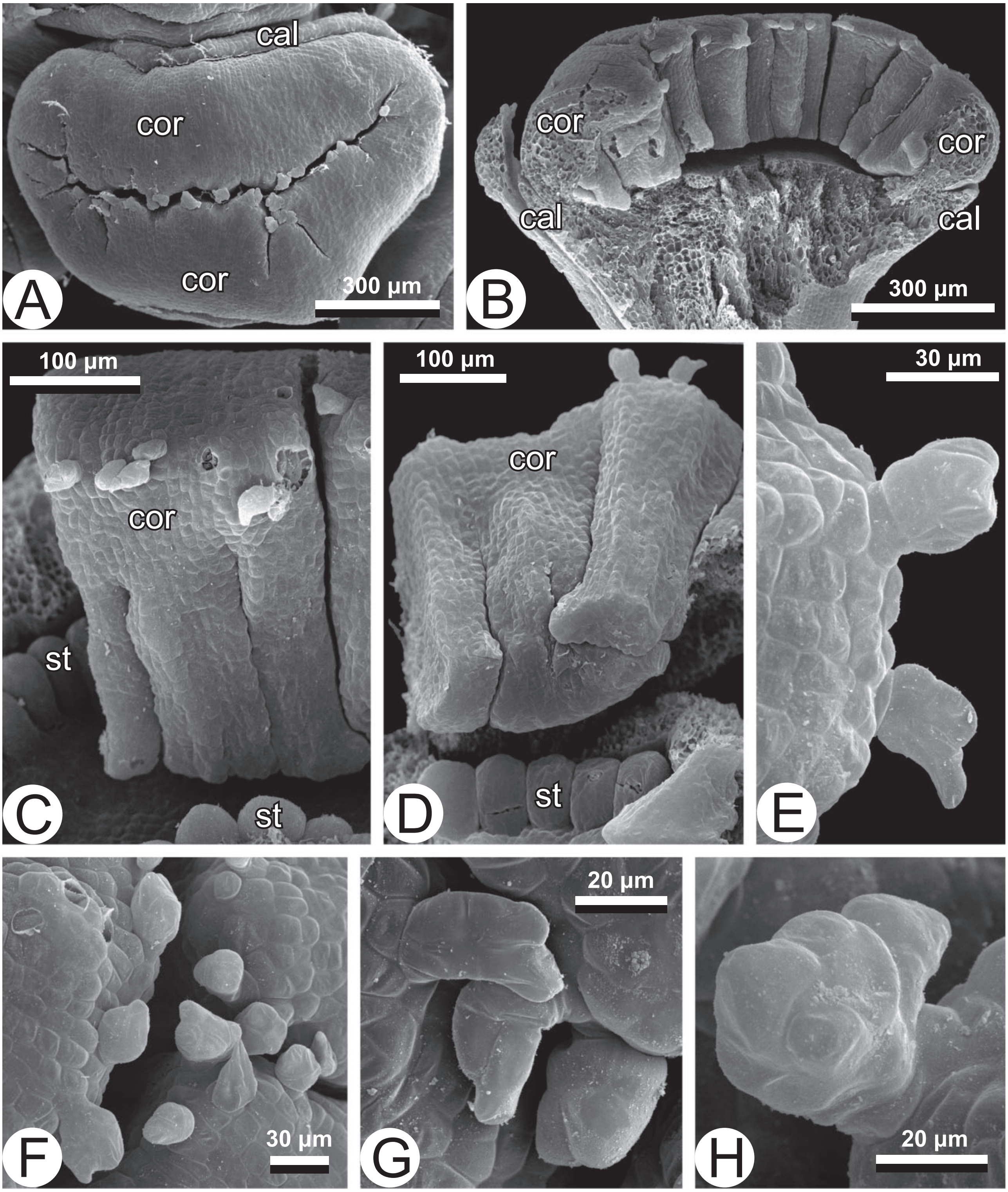

Figure 18. Details of corolla structure before the gynoecium development. A, corolla top view. B, longitudinal section of corolla. C, part of corolla viewed from inside showing the folds. D, part of the corolla artificially bent outwards and viewed from the inside showing the apical margin facing floral meristem. E, special hairs along the fusion surface of corolla from (D). F–H, special hairs along the corolla suture, top view. Cal, calyx; cor, corolla; st, stamen.

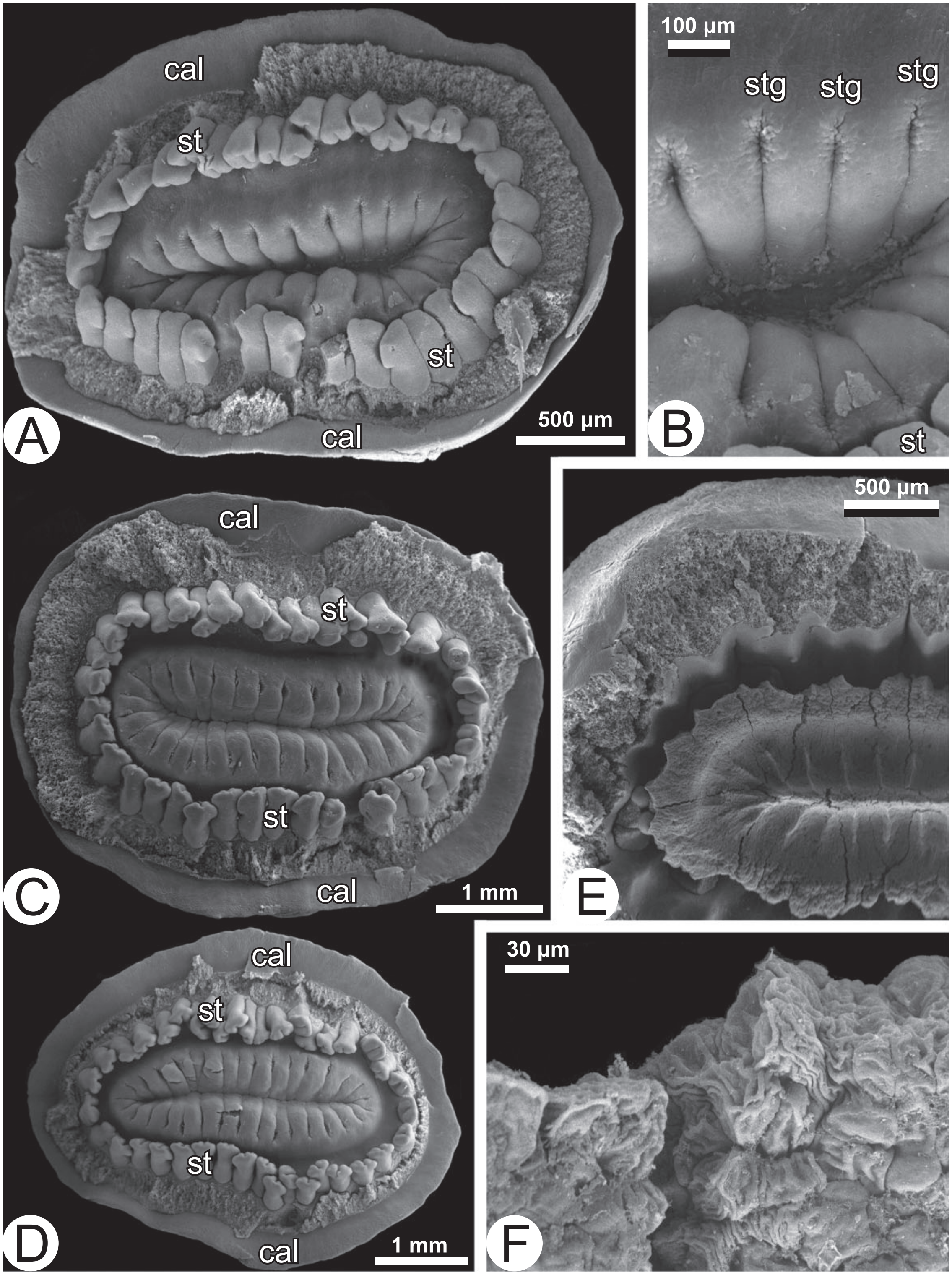

Figure 19. Final stages of flower development of *Schefflera subintegra* from Phu Rua. A, flower before the postgenital fusion of ventral carpel sides within symplicate zone of the gynoecium, corolla removed. B, part of gynoecium from (A), note the roof of synascidiate zone of the gynoecium visible through the unfused symplicate zone. C, D, flower after closure of symplicate zone of the gynoecium, corolla removed. E, part of calyptra at the same stage of development as (C) and (D), viewed from below; note the trace of appressed style in its centre and traces of stamens around it. F, close-up of calyptra in (E) showing the postgenital fusion of the folds in its central (apical) part. Cal, calyx; st, stamen; stg, stigma.

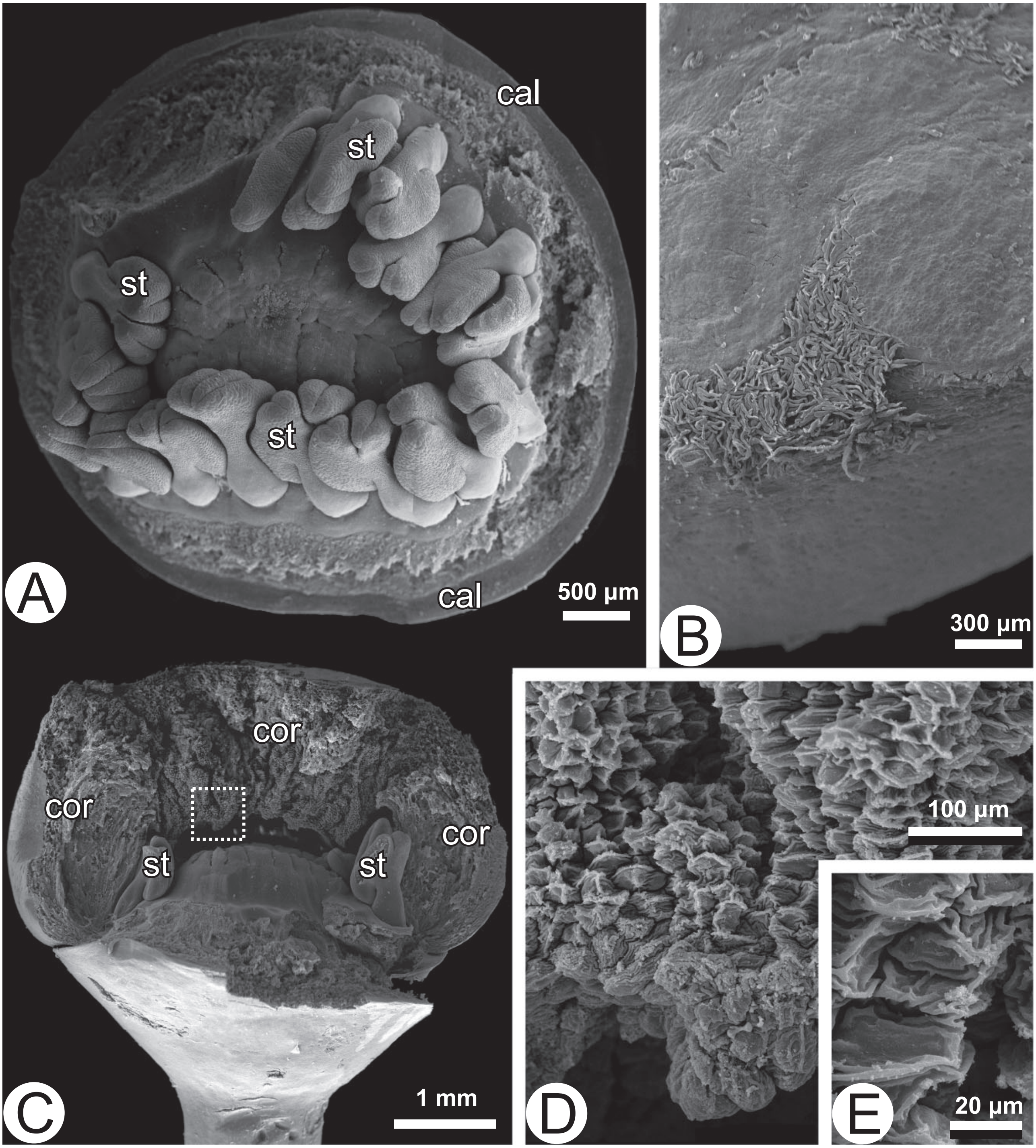

Figure 20. Structure of almost mature flower of *Schefflera subintegra* from Doi Inthanon. A, flower top view, corolla removed. B, outer surface of calyptra showing dense stellate indumentum in the area free from the pressure of other structures of the inflorescence. C, flower side view, calyptra partly removed; note the stamens and the style tightly appressed to the calyptra. D, close-up of the region contoured in (C) showing the cell wall sculpture at the area of postgenital fusion of abaxial corolla surfaces. E, details of the ribbed sculpture. Cal, calyx; cor, corolla; st, stamen.

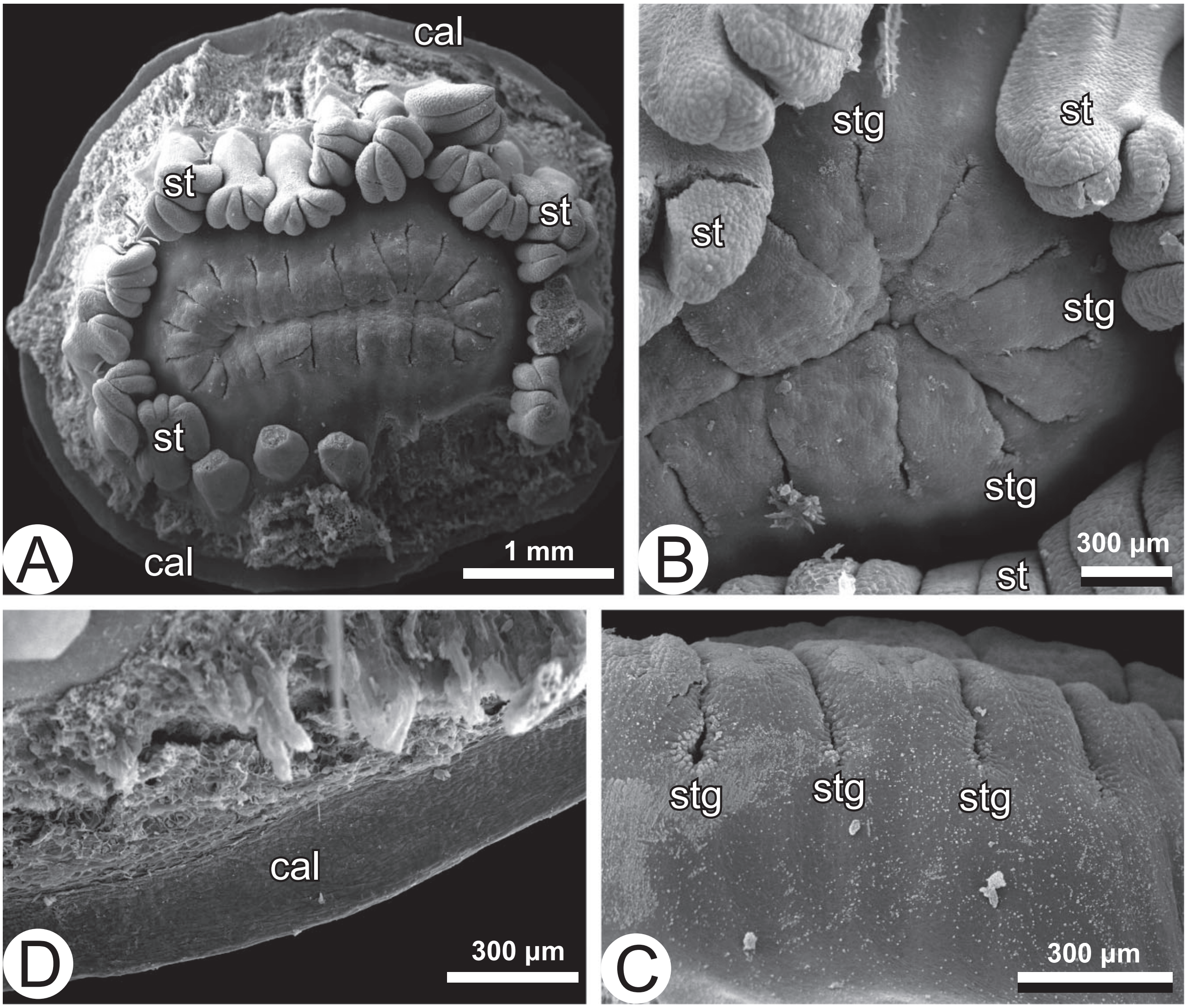

Figure 21. Structure of almost mature flower of *Schefflera subintegra* from Doi Inthanon. A, flower top view, corolla removed. B, part of the gynoecium viewed from above showing the disymmetric manner of carpel arrangement. C, side view of style. D, top view of calyx. Cal, calyx; st, stamen; stg, stigma.

free of postgenital fusion) (Figs 13, 14C–E). The hairs start to develop evenly on this surface but are aborted at the areas which are adpressed to other organs (calyx, bracts or bracteoles) within the inflorescence bud (Figs 13A, C, 14C, D). Thus, only certain areas of the calyptra possess a dense indumentum whereas others appear glabrous (Fig. 20B). Stellate hairs firstly arise at the base of the calyptra and then gradually appear up to its top. The calyptra is more or less glabrous until flower opening, except the region around the suture of postgenital closure (at least in specimens from Thailand). Under-developed stellate hairs of the outer calyptra surface sometimes resemble the hairs that take part in the postgenital closure in their shape (Fig. 13C–F). Stomata are also formed on the outer corolla surface; besides, they appear on the morphologically apical corolla part which faces the style in the vicinity of the inner suture of postgenital closure. Although the precise border between adaxial and abaxial corolla sides is ambiguous as a result of the absence of a pronounced apical margin, the stomata-bearing part of the inner corolla surface is most probably the upper part of adaxial corolla side.

There is a long plastochron between the initiation of petals and stamens, and a shorter plastochron between the appearance of stamen primordia and carpel initiation. Stamen primordia arise simultaneously and just before the postgenital closure of the corolla. They are crowded in one whorl and therefore compressed on the sides, being almost quadrangular (Figs 10A–E, 15A–E). During further development, stamens outgrow the space available in the whorl and some of them appear to be slightly moved out of it, to the inner and outer sides (Fig. 19A, C, D). Each stamen develops an anther with two thecae and a short filament, which elongates during the latest stages.

The gynoecium starts to develop after corolla closure but before the fusion of its surfaces (Figs 16, 17). In accordance with the narrowly elliptic shape of the floral apex, the gynoecium arises as an elongate whorl of carpels arranged into two rows along the transversal plane of the flower (i.e. along its broader dimension) (Fig. 11). In some cases, carpels are initiated along a more complex shape (Fig. 16B). The carpels tend to alternate with the stamens; however, a precise alternation is impossible as a result of the absence of strict isomery of these whorls (Figs 12A–D, 17C, D). The synascidiate zone of the gynoecium develops first (Figs 16A–E, 17C, D). At this stage, each carpel possesses the appearance of a narrow radial depression, which represents an immature ovary locule (Fig. 11F). At the late stages of flower development, the symplicate zone arises and a narrow area of synascidiate zone can be visible for a short time in the flower centre between the rows of the plicate carpel zones (Fig. 19A, B). At this stage, the corolla is almost completely developed; it is twice as high as the ovary and considerably broader (Fig. 20C). Each carpel is congenitally united with two neighbouring carpels along the full length in the symplicate zone. The ventral suture of the plicate zone of each carpel closes and the ventral sides of carpels of the opposite rows unite postgenitally. The symplicate zone of the gynoecium forms the upper part of the ovary with a disk and a style, both bearing stomata, which most probably serve as nectar slits (Vezza *et al*., 2006; Nepi, 2007; Erbar & Leins, 2010). Stigmas develop at the highest level of the ventral suture of each carpel (Fig. 21B, C).

During the final stages of flower growth, the ovary greatly enlarges and eventually exceeds the calyptra in its height. Calyx growth slows down early and its development soon becomes arrested (Figs 20A, 21A, D). The calyx remains glabrous adaxially and usually abaxially (except the specimens from Chu Yang Sin NP; see below) and does not bear any stomata. During the final stages of calyptra growth, it does not thicken any more but enlarges intercalarily so that its apex becomes distant from the gynoecium, and the appeared space is filled with growing stamens.

The Vietnamese population (from Chu Yang Sin NP) appears to be a more pubescent variety of *S. subintegra*, though its open flowers were not observed. (1) By contrast to other specimens examined, the calyx of the Vietnamese specimens possesses an indumentum, which appears at the anther differentiation stage (Fig. 14A, B). It consists of sparse stellate or tree-shaped hairs at the edge of the calyx tube and also of stellate hairs at its abaxial surface, which are crowded in separated spots continuing the indumentum of the ovary. The ovary of the Vietnamese specimens is also significantly more pubescent than that of the Thai specimens since most of the ovary surface remains glabrous in the latter. (2) The Vietnamese population shows an extremely early development and higher density of special hairs, which contribute to the closure of the corolla orifice. The first of these hairs appear shortly after corolla initiation, when the undifferentiated floral apex is visible (Fig. 7A–E). They are initially arranged into a waved circle (or belt) at the upper surface of the thick corolla tube. The early development of these hairs may indicate that the precise border of the area of postgenital closure is spatially patterned long before the opposite corolla sectors become contiguous (but the hairs are sometimes also found below the border of fusion at later stages; Fig. 10D, G). (3) The stellate hairs of the outer corolla surface are especially dense in Vietnamese plants (Fig. 14C–E). They also appear early in development and become visible approximately at the stage of carpel initiation (Figs 11A–C, 13).

OBSERVATIONS BASED ON HERBARIUM MATERIAL

Schefflera subintegra s.l. (S. angkae and S. subintegra s.s.)

The type material of *S. subintegra* (*Kerr 15231*, K) was collected in peninsular Thailand (Trang prov., Kao Sung), whereas *S. angkae* is known from northern Thailand (Chiang Mai prov., Doi Inthanon National Park, including the type material *Kerr 5348*, K), north-eastern Thailand (Chaiyaphum prov., Phu Khieo Wildlife Sanctuary), and southern Vietnam (Kon Tum and Lam Dong prov.). Collections of *S. subintegra s.l.* are known, in addition to these localities, from peninsular Malaysia (Pahang and Perak States), north-eastern Thailand (Loei prov., Phu Rua National Park), and southern Cambodia (Kampong Speu and Kampot prov.). The researchers who explicitly accepted *S. angkae* as distinct from *S. subintegra s.s.* (Grushvitzky & Skvortsova, 1973; Shang, 1984; Grushvitzky *et al*., 1985, 1988) did not cite or annotate any specimen of the latter taxon except from the type collection.

Among the specimens of *S. subintegra* and *S. angkae* examined, we found no considerable variation in the features suggested by Grushvitzky & Skvortsova (1973) to distinguish these species, including androecium and gynoecium merism (which varies rather gradually) and style shape (which is always elliptic in cross-section). Both specimens in the type collection of *S. subintegra* (*Kerr 15231*) bear floral buds, and observation of the important floral features is only available for the flowers that were opened and cut by Grushvitzky & Skvortsova for the comparative study on which their detailed description (1973) is exclusively based. Style shape in cross-section of dry flowers is distinctively elliptic to almost round but in all cases with nonradial carpel arrangement. The stamen scars are narrowly elliptic in these specimens and circular in all others.

It is important to note that Grushvitzky and Skvortsova never collected *S. subintegra* or *S. angkae* in natural habitats, and their descriptions and conclusions are exclusively based on examination of herbarium material. As we observed in our dry specimens and in other collections, dried flowers of these species possess a considerably modified shape. The dried flowers show an elongated style, the outline of which differs remarkably from that in living flowers, sometimes appearing almost round in the top view, whereas, in other flowers of the same plant, they stay narrowly elliptic. This phenomenon may have led to aberrations in the descriptions and drawings of Grushvitzky & Skvortsova (1973).

Schefflera polyandra

Because the type specimen of this species (*Ridley 9673*, K) bears flower buds, it is impossible to check whether or not the corolla abscises as a united calyptra. However, as is evident from the crushed flower buds, the corolla unambiguously consists of separate petals (i.e. it lacks a corolla tube formed by congenital petal fusion). Moreover, the lines delimiting the petals are clearly visible in mature flower buds.

As is evident from the type herbarium material, flowers of *S. polyandra* are polysymmetric; they are round at the top view and their petals and carpels are radially arranged in the flower cross-section. Each of the observed flowers bears eight sepals, petals, stamens, and carpels, which alternate within the adjacent floral whorls.

Frodin (Stone, 1978) assumed *S. polyandra* to be a variety of *S. ridleyi*, although this taxon was subsequently accepted as a distinct species by Frodin & Govaerts (2004). Apart from the type specimen of *S. polyandra*, Frodin identified the specimen *Burkill & Hewitt 12976* (K) from Perak as *S. ridleyi* var. *polyandra*, which was initially named *S. ridleyi*. In this plant, the flowers bear free persistent petals at anthesis, and the fruits lack distinct stamen scars. As in the type specimen of *S. polyandra*, the flowers are octomerous, isomerous, with precise alternation of whorls. Frodin identified another sheet of the collection *Burkill & Hewitt 12976* (SING) along with a specimen *Batten Pooll s.n.* (SING) as *S. ridleyi* var. *polyandra* but later changed the identification to *S. polyandra*.

MOLECULAR PHYLOGENETICS (FIG. 22)

To check possible infraspecific variability of ITS sequences, some species were studied using material from more than one population. No infraspecific ITS variation was found in *Schefflera leucantha* R.Vig., *Schefflera heterophylla* (Wall. ex G.Don) Harms, *Schefflera brevipedicellata* Harms or *Schefflera membranifolia* Bui. Other species represented by more than one accession showed certain differences between sequences obtained from different accessions. Despite the presence or absence of differences between accessions of the same species, all were retained for the phylogenetic analyses.

The length of the entire ITS region (ITS1, 5.8S, and ITS2) ranges from 618 to 622 bp in all accessions except *Schefflera macrophylla* (Dunn) R.Vig. AF229733, which is 588 bp long. The alignment comprises 628 sites, of which 91 (15%) were potentially parsimony informative and 468 were constant. The maximum parsimony analysis of the ITS data set yielded 16 trees of 232 steps, with a consistency index (CI) of 0.77 and a retention index (RI) of 0.92. Topologies of the Bayesian tree and strict consensus of shortest trees found in maximum parsimony analysis are highly similar, although some nodes found in the Bayesian analysis are weakly supported in the maximum parsimony analysis (Fig. 22).

Our data support dividing the Asian *Schefflera* clade into two subclades. Subclade 1 includes *Schefflera delavayi* (Franch.) Harms, *Schefflera fantsipanensis* Bui, *S. macrophylla*, *S. membranifolia*, *Schefflera minutistellata* Merr. ex H. L. Li, *Schefflera pseudospicata* Bui, *Schefflera rhododendrifolia* (Griff.) Frodin. Each species of this group represented by more than one accession (*S. delavayi*, *S. fantsipanensis*, *S. macrophylla*, *S. membranifolia*, *S. rhododendrifolia*) is found to be monophyletic.

Subclade 2 comprises the rest of the Asian *Schefflera* clade. Of species represented by more than one accession, *Schefflera heptaphylla* (L.) Frodin, *S. brevipedicellata* and *S. heterophylla* are found to be monophyletic. *Schefflera hypoleucoides* Harms is paraphyletic with respect to *Schefflera trevesioides* Harms and *Schefflera hypoleuca* (Kurz) Harms. The only examined accession of *S. trevesioides* does not differ from five (of nine) accessions of *S. hypoleucoides*. The two sequences of *S. leucantha* are in an unresolved position in a polytomy that includes sequences of several others species. Four examined specimens of *Schefflera venulosa* (Wight & Arn.) Harms are scattered within a group of closely related

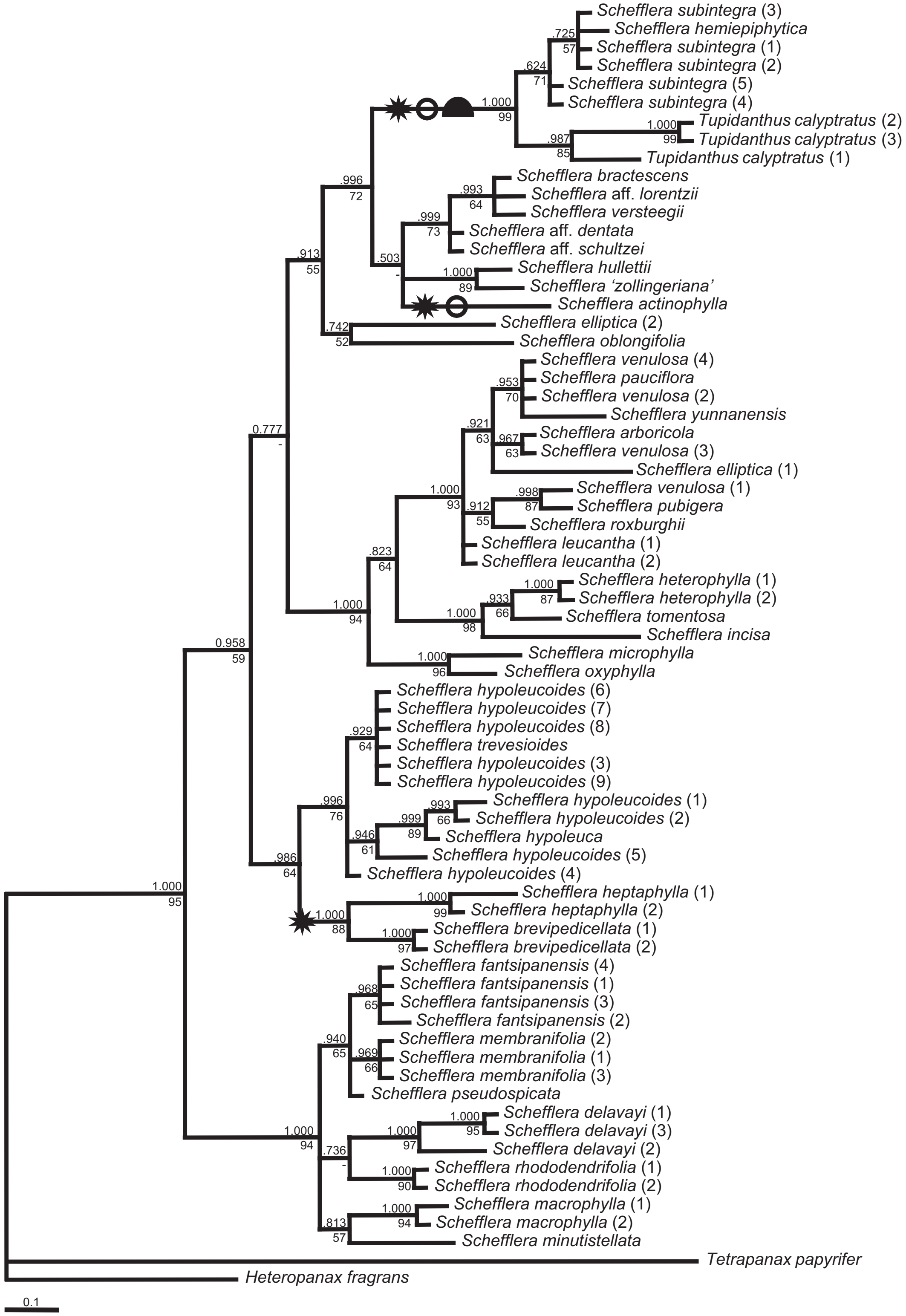

Figure 22. Bayesian tree of the Asian *Schefflera* clade based on nrITS sequences. Values above branches are posterior probabilities. Figures below branches indicate bootstrap support values obtained in maximum parsimony analysis of the same data set (only values exceeding 50% are indicated). Branch lengths are proportional to the number of the expected nucleotide substitutions. Star, evolution of floral polymery; circle, evolution of continuous calyx without free sepal lobes; dome, evolution of calyptrate corolla of congenitally united petals.

species in the subclade 2. The two GenBank accessions of *Schefflera elliptica* (Blume) Harms included in the present study occupy quite distant positions within this subclade. *Schefflera subintegra* (represented by five accessions) is found to be paraphyletic with respect to *S. hemiepiphytica* (represented by one accession that belongs to the type collection of the species).

Three accessions of *T. calyptratus* included in the analysis formed a clade, although two of them differ considerably from the third and form a long branch on the tree. Both Bayesian and maximum parsimony analysis revealed that the *S. subintegra* + *S. hemiepiphytica* clade is sister to *T. calyptratus*. Collectively, the group of these three species received a posterior probability of 1.0 and a bootstrap support of 99%. The nuclear ribosomal internal transcribed spacer (nrITS) data suggest that the closest relatives of *Tupidanthus*, *S. subintegra*, and *S. hemiepiphytica* are *Schefflera actinophylla* (Endl.) Harms, *Schefflera hullettii* (King) R.Vig., *Schefflera 'zollingeriana'*, *Schefflera* aff. *schultzei* Harms, *Schefflera* aff. *dentata* Frodin ex P.Royen, *Schefflera bractescens* Ridl., *Schefflera* aff. *lorentzii* Harms, and *Schefflera* aff. *versteegii* Harms.

DISCUSSION

Molecular phylogenetic data suggest close relationships between *S. subintegra*, *S. hemiepiphytica*, and *T. calyptratus*

Our molecular phylogenetic trees based on analyses of nrITS sequences generally do not contradict the results of Plunkett *et al*. (2005) based on the ITS+*trn*L-*trn*F markers and those of Li & Wen (2013) based on nrITS and six plastid regions. In particular, the existence of two major subclades in the Asian *Schefflera* clade is well supported. Some species represented in the present study by more than one specimen do not form monophyletic units in our trees. For example, the two GenBank accessions of *S. elliptica* do not cluster together, as in the original study of Plunkett *et al*. (2005). Four accessions of *S. venulosa* appear to be scattered among a group of several morphologically similar species. More comparative morphological and molecular data are needed to test the hypothesis of the polyphyletic nature of these species. However, these problems do not affect the major issue of the present study, namely inferring phylogenetic relationships of *T. calyptratus*. Our molecular data strongly suggest that, among the species sampled here, *S. subintegra s.l.* and *S. hemiepiphytica* are the closest relatives of *T. calyptratus*. Figure 22 illustrates possible events related to floral evolution in the Asian *Schefflera* group as inferred from molecular phylogenetic data.

The close relationship between *S. subintegra* and *T. calyptratus* revealed by molecular phylogenetics contradicts most of classifications of Araliaceae proposed for the Asian region (Harms, 1898; Li, 1942; Hoo & Tseng, 1965; Grushvitzky & Skvortsova, 1969c, 1973; Shang, 1984; Grushvitzky *et al*., 1985, 1988; Shang & Lowry, 2007) but it is in good agreement with Frodin's informal system of *Schefflera* (Frodin *et al*., 2010). Our molecular data are also congruent with results of carpological investigations of *S. subintegra* and *T. calyptratus* (Konstantinova & Suchorukow, 2010) and observations of wood anatomy of *S. hemiepiphytica* and *T. calyptratus* (Oskolski, 1994, 1995).

Striking similarity between flowers of *S. subintegra* and *T. calyptratus*

Schefflera subintegra strongly resembles *T. calyptratus* (Sokoloff *et al*., 2007) in its floral structure and development. Both species are characterized by unusually large flowers, which are much larger than those of all other members of the Asian *Schefflera* clade. Only a few other members of other clades of Araliaceae approach *Tupidanthus* in flower size (e.g. *Osmoxylon* Miq., *Trevesia*). The extraordinary flower size of *Tupidanthus* and *S. subintegra* correlates with high merism (at least in androecium and gynoecium), which is also the highest in the Asian *Schefflera* clade (Nuraliev *et al*., 2010). Then, these species share a calyptrate corolla of congenitally united petals that is unknown in other members of Araliaceae. In both species, calyptra development includes the same processes, namely complete congenital fusion of petals into a corolla tube, closure of the tube orifice by postgenital fusion of abaxial surfaces of opposite corolla parts, and appearance of hairs of a special type covering the suture of postgenital closure. Each of these traits is also unique in the Asian *Schefflera* clade, probably with *S. hemiepiphytica* as a single exception. Although flowers of *S. hemiepiphytica* are unknown so far, this species is also supposed to possess a calyptra with the same structure (see below).

Both *S. subintegra* and *T. calyptratus* (and, apparently, *S. hemiepiphytica*) are characterized by an extremely short calyx, which consists of a tube completely lacking free sepal lobes. A calyx of the same structure is also known in *S. actinophylla*, a member of the Asian *Schefflera* clade with moderately polymerous flowers (Nuraliev *et al*., 2010, 2011).

Schefflera subintegra and *T. calyptratus* also show a peculiar mode of carpel arrangement. As a result of distortion or folding of the whorl, the carpels are lined up along the transversal plane or along a more complex shape. This feature makes the flowers disymmetric (sometimes mono- or asymmetric) with transversal and median planes of symmetry, with transversal floral diameter exceeding the median diameter. Although a disymmetric mature gynoecium with two opposite rows of carpels at the level of their symplicate zone occurs in some other Asian *Schefflera* spp. (Nuraliev *et al*., 2010, 2011), only *S. subintegra* and *T. calyptratus* show nonradial carpel arrangement from the beginning of their development. As a result, the gynoecium disymmetry in these two species, unlike other Asian *Schefflera* spp., is also evident in cross-sections of the synascidiate zone. Finally, only these two species in the clade possess stamen filaments which are straight in bud; in the others they are curved (Nuraliev *et al*., 2011). This is most likely a consequence of short stamen length in relation to overall flower size in these species. The co-occurrence of more then one vascular bundle in stamens found by Grushvitzky & Skvortsova (1973; Sokoloff *et al*., 2007) and distinct stamen scars (Grushvitzky & Skvortsova, 1973; present study) can be added to the list of morphological similarities shared by *S. subintegra* and *T. calyptratus*.

The double flowers, previously described for *T. calyptratus* (Rippa, 1904; Sokoloff *et al*., 2007), also occur in *S. subintegra*. By contrast to *S. subintegra*, descriptions of *T. calyptratus* lack intermediate structures between the most obvious double flowers (with separated floral whorls) and the normal flowers. The presence of double flowers in *S. subintegra* and *T. calyptratus* can be assumed as another common feature of floral morphology in these species; on the other hand, they are also known for a wide range of angiosperms, including representatives of Araliaceae such as *Hedera helix* L. (Nozeran, 1955; Eyde & Tseng, 1971, fig. 4), *Neopanax arboreus* (L.f.) Allan and *Eleutherococcus senticosus* (Rupr. ex Maxim.) Maxim. (M. S. Nuraliev and A. A. Oskolski, unpubl. data).

Teratological structures resembling stamen filaments fused to the gynoecium disk surface were found in some flowers of *S. subintegra*. We can speculate that they appear as a result of overlapping of developmental programmes of a stamen and a carpel. The same phenomenon was documented for *T. calyptratus* (Sokoloff *et al*., 2007); however, it is still not known whether these structures occur in other Asian *Schefflera* spp. because their presence can be established only by extensive search.

Although *S. subintegra* possesses the same floral structure traits as *T. calyptratus*, most of them are considerably more strongly pronounced in the latter species. The main difference between these species is the flower merism, which is on average twice as high in *T. calyptratus* than in *S. subintegra*. Consequently, the flowers of *T. calyptratus* are also twice or more times larger than those of *S. subintegra*. In *S. subintegra*, the gynoecium whorl is often compressed in the median plane of a flower but, in *T. calyptratus*, the pattern of carpel arrangement is more complex and the gynoecium whorl is folded. On the other hand, *Tupidanthus*-like carpel arrangement is also found in some flowers of *S. subintegra*, which makes the difference in gynoecium shape of these two species only quantitative but not qualitative. Depending on the precise configuration of the folded gynoecium whorl, flowers of *T. calyptratus* and *S. subintegra* can be formally described as possessing two, one or no symmetry planes (i.e. di-, mono- or asymmetric: Neal, Dafni & Giurfa, 1998; Endress, 1999, 2001, 2006, 2012; Giurfa, Dafni & Neal, 1999; Kalisz, Ree & Sargent, 2006; Jabbour, Nadot & Damerval, 2009; Citerne *et al*., 2010; Leins & Erbar, 2010); on the other hand, flowers of these species with diverse symmetry certainly bear no significant morphological or functional differences.

Schefflera subintegra also differs from *T. calyptratus* in the flower shape at the earliest stages of its development. In *T. calyptratus*, its peculiar flower shape (and therefore nonradial flower symmetry) is present from the stage of floral primordium and remains constant throughout development (Sokoloff *et al*., 2007). In *S. subintegra*, the developing flower is circular in outline (polysymmetric) until the corolla tube completely covers the undifferentiated floral centre. Only then does the flower become wider transversally. In accordance with the terminology of Endress (1999, 2012), the flower of *S. subintegra* is disymmetric with early polysymmetry. Despite these structural differences, the flowers of both *S. subintegra* and *T. calyptratus* most probably correspond to the actinomorphic flower type in respect of their pollination ecology.

Mature flowers of *S. subintegra* are characterized by well-pronounced styles (Craib, 1930), whereas styles are completely absent in flowers of *T. calyptratus* (Sokoloff *et al*., 2007, figs 2–5). The style of *S. subintegra* is sometimes interpreted as a short stylopodium (Grushvitzky & Skvortsova, 1973; Frodin *et al*., 2010; Konstantinova & Suchorukow, 2010). The presence or absence of the style (or free stylodia) was regarded for a long time as an important taxonomic feature and was used in a number of systems for delimitation of subgeneric taxa in *Schefflera* (Viguier, 1906, 1909; Hoo & Tseng, 1965; Grushvitzky & Skvortsova, 1969a,b,c; Shang, 1984; Grushvitzky *et al*., 1985). The species belonging to other groups of the Asian *Schefflera* clade show significant differences in length of their styles (Shang & Lowry, 2007; Konstantinova & Suchorukow, 2010; Nuraliev *et al*., 2011). These differences might have certain impact on flower ecology. Moreover, in *T. calyptratus*, a style-like structure arises during fruit maturation (M. S. Nuraliev, unpubl. data), whereas, in *S. subintegra*, the style disappears by the time of fruit maturation as a result of differential growth of the ovary roof. The style identity and its morphogenetic and taxonomic significance in the Asian *Schefflera* clade requires further investigations (Li & Wen, 2013).

Flowers of *T. calyptratus* differ from those of *S. subintegra* in having lenticels on the outer surface of the ovary wall. However, this difference is most probably a developmental result of large flower size in *T. calyptratus*, rather that an independently acquired new morphological character. In angiosperms, lenticels commonly occur on woody stems. At least in Araliaceae, there appears to be a threshold organ size after which induction of the developmental program of lenticels (and periderm) takes place, regardless of the organ identity (e.g. on massive petioles).

We consider that *T. calyptratus* and *S. subintegra* should be classified in the same genus and section as a result of their significant morphological similarity, which is congruent with molecular phylogenetic trees. Whether they should form the oligospecific *Tupidanthus* or be treated as an oligospecific section of a larger genus (e.g. *Heptapleurum* Gaertn., which has a nomenclatural priority over *Tupidanthus*) should be decided in the course of the ongoing taxonomic disintegration of the clearly polyphyletic *Schefflera s.l*.

SCHEFFLERA ANGKAE DOES NOT DIFFER REMARKABLY FROM *S. SUBINTEGRA* AND DOES NOT MERIT RECOGNITION AS A TAXON

As Grushvitzky & Skvortsova (1973) suggested, *S. angkae* is distinguished from *S. subintegra* by higher floral merism and a style that is elliptic in cross-section (versus rounded in the latter species). Our data show, however, that the figures of floral merism cannot be considered as markers for reliable delimitation of these species. According to the diagnoses compiled by Grushvitzky & Skvortsova (1973), there are 16–22 stamens and 14–20 carpels in flowers of *S. subintegra s.s.* versus at least 23 stamens and 20 carpels in flowers of *S. angkae*. The specimen from Doi Inthanon NP (which is the modern name of Doi Angka, the *locus classicus* of *S. angkae*) examined in the present study shows, however, a number of floral parts that covers merism intervals stated for both these species (i.e. 19–29 stamens and 15–27 carpels). Furthermore, Craib in his description of *Scheffleropsis subintegra* var. *angkae* (see Grushvitzky & Skvortsova, 1973) reported 18 ovary locules, which is typical for *S. subintegra s.s.* according to Grushvitzky & Skvortsova (1973). Our study (including examination of herbarium collections) shows that no other feature can be used to distinguish these taxa reliably. We found uniformly elliptic styles only in the type specimen of *S. subintegra* that could be a result of its drying during herbarization; all other specimens examined have rounded styles. Thus, our data strongly support earlier ideas (Frodin & Govaerts, 2004) on the absence of any differences between *S. angkae* (= *Scheffleropsis subintegra* var. *angkae*) and *S. subintegra*. The conclusion of a relatively low flower merism of *S. subintegra s.s.* by Grushvitzky & Skvortsova (1973) appears to be unreliable because it was based on examination of several flowers from one or two inflorescences of a single tree, and all Araliaceae representatives with polymerous flowers (including *T. calyptratus* and *S. subintegra s.l.*) are known to show considerable variation in the number of floral parts (e.g. Eyde & Tseng, 1971; Nuraliev *et al*., 2010). Moreover, specimen identification by various researchers of Asian Araliaceae (I.V. Grushvitzky with collaborators, N.-S. Bui, C.-B. Shang, and others; M. S. Nuraliev, unpublished observations) appeared to be rather confusing and controversial. Although the present study confirmed the presence of narrowly elliptic stamen scars only in the type specimen of *S. subintegra*, in contrast to circular scars in all other specimens of *S. subintegra s.l.* or *S. angkae* (Grushvitzky & Skvortsova, 1973, fig. 5), this difference alone does not appear to be sufficient for identifying separate taxa, in one of which it was observed in only one individual; furthermore, the specimen of *S. subintegra* was examined in dry conditions, which could result in a modified shape of the scars.

Because the type specimen of *S. subintegra* cannot be included in molecular analysis as a result of its age, only morphological features are available for solution of the question regarding separation of this species with *S. angkae*. Then, the geographical distribution of the specimens also does not contradict aggregation of these two species, although *S. subintegra s.s.* occupies the edge of the range of *S. subintegra s.l.* and its location is not in the area of distribution of *S. angkae*. A complex of arguments provided above supports Frodin's decision (Frodin & Govaerts, 2004) to include *Schefflera angkae* (= *Scheffleropsis subintegra* var. *angkae*) in *Schefflera subintegra*.

SCHEFFLERA HEMIEPIPHYTICA REMAINS THE CLOSEST RELATIVE OF *S. SUBINTEGRA*

Schefflera hemiepiphytica is currently the most enigmatic species of the former genus *Scheffleropsis*. No progress in understanding its reproductive morphology or geographical distribution has been reported since its description by Grushvitzky & Skvortsova (1973). Our molecular phylogenetic data confirm its position close to *S. subintegra s.l.* However, *S. hemiepiphytica* is nested in *S. subintegra* in molecular phylogenetic trees, which do not support treatment of the former as a separate species. These species share such important features as considerable floral polymery and a more or less disymmetric gynoecium. *Schefflera hemiepiphytica* differs from *S. subintegra s.l.* at least by hairy stigmas and less numerous carpels (Grushvitzky & Skvortsova, 1973). Although perianth morphology of *S. hemiepiphytica* remains unknown, the presence of a calyptrate corolla is quite possible in this species, as its phylogenetic position and the absence of individual scars of abscised petals suggest.

SCHEFFLERA SIAMENSIS AS ADDITIONAL POTENTIAL RELATIVE OF *S. SUBINTEGRA*

Schefflera siamensis W.W.Sm. ex Craib represents another poorly known Asian *Schefflera* species known only from the type material (*Kerr 2281*, collected in 1913, BM, E, K) bearing inflorescences with fruits and from several subsequent specimens (the most recent is a sterile specimen by *Callmander 1047*, collected in 2012, BKF, G, MO). Both specimens cited above are collected in Doi Chiang Dao (Thailand). Although described as early as 1918 (Craib, 1918), this species was never included in any regional taxonomic revisions. The relationship of *S. siamensis* to *S. subintegra*, and *T. calyptratus* was indicated in Frodin's informal system, where it was at first placed into group '*Sciodaphyllum*' subgroup '*Tupidanthus* 2', whereas *S. subintegra* and its allies were placed into subgroup '*Tupidanthus* 1' (Plunkett *et al*., 2005). Later, Frodin placed all these species together within group '*Brassaia*' subgroup '*Tupidanthus* 1' (Frodin *et al*., 2010). *Schefflera siamensis* is characterized by inflorescences in a lateral position and a slightly polymerous gynoecium with ten to 12 locules (Craib, 1918). This description does not contradict its putative close phylogenetic position to *S. subintegra*, which was also reported by Grushvitzky & Skvortsova (1973) as possessing lateral inflorescences (which are most probably morphologically pseudo-lateral because truly lateral inflorescences are not found in Araliaceae; Shang & Lowry, 2007), with other species of the former genus *Schefferopsis*. On the other hand, this combination of features is known for several other Asian *Schefflera* spp. [e.g. *S. brevipedicellata* and *S. khasiana* (C. B. Clarke) R.Vig.] (Shang & Lowry, 2007). Phylogenetic data do not indicate close relationships between *S. brevipedicellata* and *S. subintegra* despite similarities in these characters. Clearly, *S. siamensis* will remain imperfectly known until collected with flowers (or flower buds) and included in molecular phylogenetic analyses.

SCHEFFLERA POLYANDRA AND ITS DOUBTFUL RELATION TO *S. SUBINTEGRA*

The close relation of *S. polyandra* to other species of the *Scheffleropsis* group was postulated as a result of its polymerous flowers and calyptrate corolla (Grushvitzky & Skvortsova, 1973). However, Frodin (Stone, 1978) treated this taxon as *Schefflera ridleyi* var. *polyandra* and indicated floral merism as the only difference between var. *ridleyi* and var. *polyandra*. The type of *S. ridleyi* has hexamerous flowers (Stone, 1978), probably sometimes with pentamerous corolla (King, 1898), whereas flowers of *S. polyandra* are octomerous (Grushvitzky & Skvortsova, 1973), probably sometimes heptamerous (Stone, 1978). As found by Grushvitzky & Skvortsova (1973) and confirmed by our re-examination of type material, Ridley erroneously described the androecium of *S. polyandra* as 14- to 16-merous (and its corolla as pentamerous). This error was reproduced by Frodin (Stone, 1978). Revealing the isomerous nature of flowers of *S. polyandra* further supports the conclusion of Frodin that this species is much more closely related to *S. ridleyi* (and therefore to the other species of the '*Parapanax*' group, which is characterized by a floral groundplan close to that typical for Asian *Schefflera* spp.; Frodin *et al*., 2010) rather than to any of species of *Scheffleropsis* group. Furthermore, moderate floral polymery (with not more than 15 elements in each whorl) is known for a significant number of representatives of the Asian *Schefflera* clade, which were never considered in such segregate taxa as *Tupidanthus*, *Scheffleropsis*, *Brassaia* or *Cephaloschefflera* Merr. (Shang & Lowry, 2007; Frodin *et al*., 2010).

The calyptrate corolla was considered by Grushvitzky & Skvortsova (1973) as one of the main features of *Scheffleropsis*. During examination of the type specimen of *S. polyandra*, we found no traits of congenital petal fusion. This means that the 'calyptra' of this species (if it is indeed present) described by Ridley (1922) can only be developed by postgenital adhesion of petal lateral margins and/or apices. Such a calyptra-like structure is known in some other Asian *Schefflera* spp., e.g. *Schefflera incisa* R.Vig. (Sokoloff *et al*., 2007; Nuraliev *et al*., 2011), which possesses pentamerous flowers and is only distantly related to *S. subintegra* and *S. hemiepiphytica* in our molecular phylogenetic tree. In *S. incisa*, petal morphology and anatomy is equal to that of 'typical' *Schefflera* spp. with free petals (Nuraliev *et al*., 2011). In the absence of congenital petal fusion, the corolla of *S. polyandra* crucially differs from a true calyptra, which is known for *T. calyptratus* (Sokoloff *et al*., 2007; Nuraliev *et al*., 2009) and *S. subintegra s.l.* (present study).

The absence of congenital petal fusion in *S. polyandra* explains how the petals were counted for this species (Ridley, 1922; Grushvitzky & Skvortsova, 1973). The corolla of eight petals reported for *S. polyandra*, was considered by Grushvitzky & Skvortsova (1973) as a diagnostic feature for the whole genus

Schefferopsis but without a reasonable basis. In fact, corolla merism of *S. subintegra s.s.* was not indicated in the original description (Craib, 1930) and is not evident from its collections; flowers of *S. angkae* and *S. hemiepiphytica* were unknown at the time of the revision by Grushvitzky & Skvortsova (1973). As shown in the present study, the corolla of *S. subintegra* (including *S. angkae*) and probably *S. hemiepiphytica* (see below) bears no evidence of individual petals.

Although Grushvitzky & Skvortsova (1973) placed *S. polyandra* with *S. subintegra* and two other species in *Schefferopsis*, they placed *S. polyandra* in a separate section than the other species of the genus. One of the reasons for this separation was the single vascular bundle in stamen filament of *S. polyandra* (in contrast to three bundles in other representatives of the genus), a feature common in most other Asian *Schefflera* spp. The lack of distinct stamen scars in *S. polyandra* was also noted to be a unique feature in *Schefferopsis* and common with *Schefflera* spp. (Grushvitzky & Skvortsova, 1973). *Schefferopsis polyandra* also resembles 'typical' Asian *Schefflera* spp. in having polysymmetric flowers, whereas flowers of *S. subintegra s.l.* (present study) and *S. hemiepiphytica* (Grushvitzky & Skvortsova, 1973, fig. 5) are disymmetric.

Summarizing all the differences described above, we conclude that *S. polyandra* and *S. subintegra* with its allies are not likely to be closely related. Both main distinctive features of the genus *Schefferopsis* appear not to be unique for its species: floral merism and corolla structure similar to those of *S. polyandra* are found also in certain *Schefflera* spp. Furthermore, both these features show remarkable variation in the species of the former *Schefferopsis*, which is in fact highly heterogeneous if circumscribed based on these characteristics. We consider that the genus *Schefferopsis* with the limits proposed by Grushvitzky & Skvortsova (1973) cannot be segregated as a taxon of any rank.

PUTATIVE MORPHOLOGICAL HETEROGENEITY OF *S. SUBINTEGRA*

Our data suggest that local populations of *S. subintegra s.l.* differ from each other in floral merism. The individual of *S. subintegra s.l.* collected in Doi Inthanon NP has lower numbers of floral parts (19–29 stamens, 15–27 carpels) than the samples from Phu Rua NP (26–42 stamens, 18–33 carpels) and especially from Chu Yang Sin NP (32–43 stamens, 25–31 carpels). The infraspecific variation of these numbers needs further examination on more representative sampling, which can clarify, among other things, the taxonomic value of meristic characters for this group. Furthermore, *S. subintegra s.l.* appears to occupy a paraphyletic position in relation to *S. hemiephiphytica* in our molecular phylogenetic tree, which raises the possibility of heterogeneity of the former taxon. However, potential ways to break up *S. subintegra s.l.* most probably have nothing to do with the previously suggested delimitation into *S. angkae* and *S. subintegra s.s.* The differences in calyx and ovary pubescence and in density and timing of development of special corolla hairs between specimens from Phu Rua NP and Chu Yang Sin NP described here appear to be useful features in resolving this problem.

EVOLUTIONARY PATHWAYS THAT LEAD TO APPEARANCE OF FLOWERS OF *S. SUBINTEGRA* AND *T. CALYPTRATUS* ARE HIGHLY UNUSUAL FOR THE ASIAN *SCHEFFLERA* CLADE

Increased floral merism

Because most of Asian *Schefflera* spp. (and most Araliaceae) possess penta- or hexamerous flowers (Harms, 1898, 1921; Viguier, 1909, 1923; Li, 1942; Shang, 1984; Shang & Lowry, 2007), we define a species with polymerous flowers as one that normally has seven or more elements in at least one floral whorl. Following this definition, we found three clades in the Asian *Schefflera* clade in our molecular phylogenetic tree, in which floral polymery has evolved and should be considered as a synapomorphy: (1) *S. brevipedicellata* + *S. heptaphylla* with a gynoecium of six to 15 carpels and merism of other whorls within or below this range; (2) *S. actinophylla* [and probably other species of the *Schefflera* section *Brassaia* (Endl.) Tseng & Hoo, not included in the analysis; Frodin, 1975] with nearly 12-merous corolla, androecium, and gynoecium; and (3) (*S. subintegra s.l.* + *S. hemiepiphytica*) + *T. calyptratus* with androecium and gynoecium merism varying from (eight) ten carpels in *S. hemiepiphytica* to up to approximately 200 stamens and carpels in *T. calyptratus*. Such homoplastic evolution of floral merism allows the characterization of this feature as unstable and easily changeable in Asian *Schefflera* clade. The homoplastic nature of evolution of gynoecium merism in various clades of angiosperms has also been highlighted by Endress (2014). Moreover, in all the angiosperm families with an occurence of high carpel numbers, taxa 'with the highest carpel numbers are always phylogenetically highly nested' (Endress, 2014). The flexibility of regulation of floral merism in Asian *Schefflera* clade is also evident from slightly polymerous flowers that are rarely observed in the species with normally pentamerous flowers; in such individuals, abnormal and normal flowers develop within the same inflorescence (M. S. Nuraliev, unpubl. data).

Notably, *T. calyptratus* being the species with the highest floral merism among the Asian *Schefflera* clade occupies a sister position to a clade comprising species with moderately polymerous flowers (*S. subintegra s.l.* + *S. hemiepiphytica*). This supports the idea that its flower has probably not evolved directly from pentamerous flowers but undergone an intermediate stage in merism increase.

Reduced calyx

Although no strict developmental or evolutionary explanation can be provided for the strong reduction of the calyx with complete loss of free sepal lobes in *S. subintegra* and *T. calyptratus*, it can be noted that this feature is not rare in species of Araliaceae with a polymerous gynoecium. It is known in *S. actinophylla* with 12 carpels (Nuraliev *et al.*, 2010, 2011) and outside the Asian *Schefflera* clade in the genus *Osmoxylon*, in which fertile flowers sometimes possess a multilocular ovary (Philipson, 1979). Thus, we tentatively assume the calyx reduction to be an effect of the same regulation patterns that are responsible for gynoecium polymery. On the other hand, the co-occurrence of a moderately polymerous gynoecium and a calyx of small but distinct sepals (at least in early developmental stages) are known in the large genus *Plerandra sensu* Lowry, Plunkett & Frodin (2013), also known as the Melanesian *Schefflera* clade [i.e. in many species of *Plerandra* subgenus *Plerandra* and in *P. plerandroides* (R.Vig.) Lowry, G. M. Plunkett & Frodin of subgenus *Dizygotheca* (N.E.Br.) Lowry, G. M. Plunkett & Frodin] (Nuraliev *et al.*, 2010, fig. 35; Oskolski *et al.*, 2010a, 2011). In addition, complete loss of any visible traces of sepals has been documented in pentamerous flowers of some species of *Hydrocotyle* L. (Erbar & Leins, 1985, 2004; Leins & Erbar, 2004; Nicolas & Plunkett, 2009). According to Endress (2008), reduced organs that have decreased in size and lost their original function may become labile in number and shape because functional constraints on shape are lacking. From this point of view, the loss of free sepal lobes can be considered as an extreme expression of variation of calyx merism with smoothing (or even loss) of morphological boundaries between individual sepals. This speculation is consistent with the absence of protective function of calyx in *S. subintegra* and *T. calyptratus* and its relatively small size at all stages of floral development.

Calyptrate corolla

Schefflera subintegra and *T. calyptratus* (and probably *S. hemiepiphytica*) are most likely the only reported representatives of Araliaceae which possess a calyptra formed by congenitally united petals. Counting petals in these species is impossible because the petals are congenitally united throughout their length during all developmental stages, and the structure of the corolla tube is completely homogeneous. The only structures that could be considered as presumable traits of individual petals are the folds at the corolla rim. These folds are more pronounced in *S. subintegra* than in *T. calyptratus*. However, the irregular shape and density of these folds in *S. subintegra* with their highest number in the narrowest parts of the tube leads us to consider them as no more than a mechanical effect of the corolla bending. As Endress (2011: 1477) suggested, ‘if an annular young plant part that spans an opening of a certain diameter in early development needs to close in later development, i.e. to form a closed pore, it can do this only by lobation (in the longitudinal direction) or by irregular thickening, which also leads to a sort of lobation (in the transverse direction), or by both processes in combination’; in other words, lobe formation is unavoidable in such cases for geometrical reasons. Our example of lobation during the closure of the corolla tube in *S. subintegra* perfectly suits this conclusion. We question whether petals in *S. subintegra* and *T. calyptratus* have completely lost their individuality, and their corolla could be characterized as continuous instead of consisting of petals (i.e. with no merism). This hypothesis is to be tested by investigation of corolla anatomy and spatial patterns of regulatory gene expression. In evolutionary terms, petals within the corolla of these species are extremely synorganized (i.e. they are connected to form a single functional system and evolutionary unit) (Endress, 1990, 2006).

The calyptra of congenitally united petals possibly also occurs in some species of *Schefflera* section *Brassaia*. For example, a calyptrate corolla with short free petal apices is reported for *S. megalantha* Harms (Harms, 1921), although direct developmental data are absent. Corolla diversity in this group needs a comprehensive morphological investigation; nevertheless, it is clear that the calyptra in section *Brassaia*, if it is indeed present in the same way as in taxa examined in the present study, has evolved independently in relation to that of *S. subintegra* and *T. calyptratus*.

The specific ribbed sculpture of cell walls of the abaxial corolla epidermis in the area of postgenital fusion in *S. subintegra* is also found in other Asian *Schefflera* spp. (Nuraliev *et al.*, 2011, fig. 2A, C) at the lateral and upper abaxial petal surface, where it is responsible for tight petal connection in flower bud. It is noticeable that similar sculpture occurs in species with very different corolla structure, namely with free [e.g. *S. actinophylla*, *Schefflera arboricola* (Hayata) Merr., *Schefflera bodinieri* Rehder, *S. bractescens*, *S. delavayi*, *S. heptaphylla*, *S. hypoleucoides*, *S. leucantha*, *S. macrophylla*, *S. membranifolia*, *S. venulosa*; M. S. Nuraliev, unpubl. data] or congenitally united petals (*S. subintegra*; presence of this feature in *T. calyptratus* remains unknown). Moreover, certain *Schefflera* spp., such as *S. incisa* (Sokoloff *et al.*, 2007; Nuraliev *et al.*, 2011) and *S. polyandra* (present study), are reported to possess a calyptra-like corolla formed by postgenital fusion of initially free petals. In such species, petals just abscise in the same condition in which they are in bud. This evidence supports the assumption that postgenitally fused elements show only minor morphological differences from free elements (Verbeke, 1992; Sokoloff *et al.*, 2006). One can assume that the mechanism of petal connection in the flower bud in Asian *Schefflera* spp. is a precondition for development of calyptrate structures with postgenital petal fusion or postgenital closure of the corolla tube. In *S. subintegra* with congenital formation of the corolla tube, the special cell wall sculpture is not used for fusion between adjacent petals, although this mechanism is recruited for realization of a related but different process of apical closure of the calyptra.

Similar cell wall sculpture was found by Prenner (2011) in petals of *Acacia celastrifolia* Benth. (Fabales, Fabaceae). This species resembles the representatives of Asian *Schefflera* with free petals in the manner of petal connection by the abaxial sides in flower bud, in the distribution of the sculpture across the petal surface, in the presence of stomata in the petal epidermis, and in early corolla development, which indicates protective function of the corolla in both cases. Similar function of the corolla in these unrelated taxa appeared to cause a number of morphological and morphogenetic convergences.

Peculiar floral shape and symmetry

Our data on floral morphology of *S. subintegra* support the assumption that the multiplication of primordia within a single (especially inner) floral whorl leads to deviations from floral polysymmetry, often with the arrangement of the elements into an ellipse or (in cases of more pronounced polymery) into two rows (Endress, 2006, 2014; Sokoloff *et al.*, 2007; Rudall, 2008; Nuraliev *et al.*, 2010). The intact undifferentiated floral apex, which is usual for multicarpellate syncarpous monocyclic gynoecia (Endress, 2014), was observed in flowers of *S. subintegra* as a narrow depression between the carpel rows (Fig. 19B) at late developmental stages but is not prominent in mature flowers probably being enclosed by the symplicate zone of gynoecium (though its complete differentiation cannot be excluded). Disymmetric shape of gynoecium and corolla of *S. subintegra* and its corolla lobation can be assumed as being indirectly influenced by floral architecture (*sensu* Endress, 1994, 2008). According to Endress (2006), such carpel arrangement occurs in angiosperms with polymerous monocyclic syncarpous gynoecia of more than approximately ten carpels. However, Endress (2006) did not indicate whether the gynoecium polysymmetry is disturbed initially or during the carpel formation in his examples, although this is crucial for understanding of floral morphogenetic regularities. Endress (2014) summarized that, in multicarpellate flowers, the gynoecium disymmetry commonly arises during its development through differential irregular growth of different floral sectors. By contrast, in *S. subintegra* (present study) and *T. calyptratus* (Sokoloff *et al.*, 2007), the flower is already pronouncedly disymmetric at the stage of gynoecium initiation. Endress (2014) explained such deviations in gynoecium symmetry by the impossibility of precise meeting of all the carpels in the floral centre as a result of space limitaion (at least in the uppermost part of the syncarpous zone) on one hand and the necessity for compitum development on the other hand; nonpolysymmetric carpel arrangement along the unspent floral apex also allows the maintenance of a moderate size of a flower with numerous carpels. Elliptic shape is also known to be a common feature for fasciated axial structures in plants (Sokoloff *et al.*, 2007; Sinyushin, 2010; Choob & Sinyushin, 2012). Furthermore, abnormal polymerous flowers of Asian *Schefflera* spp. normally characterized by pentamerous flowers (see above) show floral shape and carpel arrangement similar to those of *S. subintegra*. Thus, the peculiar flower symmetry of *S. subintegra* and *T. calyptratus* should be regarded as a morphogenetic consequence of flower polymery and not as an evolutionary adaptation.

POSSIBLE SCENARIOS FOR THE ORIGIN OF THE *T. CALYPTRATUS* FLOWER

We distinguish two major features of flowers of *S. subintegra* and *T. calyptratus*: (1) calyptra of congenitally fused petals (including a number of morphological traits involved in its formation) and (2) considerable androecium and gynoecium polymery (together with calyx reduction and also floral shape and symmetry of a special type). According to Endress (2006), these features can be classified as ‘non-key innovations’ in *S. subintegra* and *T. calyptratus* (i.e. important morphological novelties that did not lead to the evolution of a large clade).

As a qualitative character, a calyptrate corolla (or at least congenital petal fusion) most probably appeared during a single evolutionary event directly from a corolla of free (or postgenitally united) petals. According to our molecular phylogenetic tree, it occurred once in the Asian *Schefflera* clade and represents a synapomorphy for the group ((*S. subintegra s.l.* + *S. hemiepiphytica*) + *T. calyptratus*).

Because floral merism is a quantitative character, two logical opportunities can be suggested for the evolution of polymerous flowers of *T. calyptratus* and its allies from pentamerous flowers which are plesiomorphic for the Asian *Schefflera* clade. First, floral merism could increase gradually under the pressure of positive selection in case of presence of advantages of polymerous flowers and/or fruits. Second, it could change during a single step (saltation) or several steps caused by respective number of fixed mutations (Theissen, 2006, 2009).

The flower structure of *T. calyptratus* was assumed to be a result of fasciation (Eyde & Tseng, 1971; Sokoloff *et al*., 2007), which implies a single evolutionary event (saltation). Mutations of orthologues of *CLAVATA* family genes of *Arabidopsis* Heynh. were suggested as a putative mechanism of origin of fasciated flowers of *T. calyptratus* (Sokoloff *et al*., 2007). Addition of a sister clade to *T. calyptratus*, which is characterized by moderately polymerous flowers, to the evolutionary scenario makes it necessary to assume at least two such saltations (the first at the base of the clade with polymerous flowers, expressed in the appearance of calyptrate corolla possibly simultaneously with increase in floral merism, and the second saltation in *T. calyptratus*) or to choose the gradual evolution as most plausible. Within the first choice, the flower of *T. calyptratus* should be considered as 'twice fasciated'. The plausibility of the second choice is difficult to check as a result of the low number of species in the clade with polymerous flowers. Furthermore, the difference between several successive saltations and gradual changing of the character is unclear because acceptance of discrete species leads to a stepwise view on any evolutional process.

The double flowers of various angiosperms are commonly treated as a result of fasciation (Choob & Sinyushin, 2012). From this point of view, such structures in *T. calyptratus* and *S. subintegra* should be considered as fasciation of the next order, which occurs, in contrast to the supposed inherited fasciation(s) that caused high floral merism typical for these species, during the plant ontogeny (as the double flowers are scattered among normal flowers on a plant). Depending on the degree of lateral union of the floral whorls, the double flowers can be classified as defasciation or linear (flattened) fasciation (Choob & Sinyushin, 2012).

In the narrow definition of Bateman & DiMichele (2002), saltation is a 'genetic modification that is expressed as a profound phenotypic change across a single generation'. In this concept, a species evolved by saltation should probably be regarded as a descendant of a single organism (i.e. the individual that has undergone the modification). In the case of our speculative hypothesis, this organism acts as a parent individual of the first *CLAVATA*-like gene mutant(s), which can also be defined as 'hopeful monster(s)' with a high level of fitness (Bateman & DiMichele, 2002; Theissen, 2006). Such a hypothesis is hardly testable but it appears to be obvious that saltations should occur rather rarely in plant evolution. For this reason, *T. calyptratus* is probably not a result of two successive saltations (and parasaltations *sensu* Bateman & DiMichele, 2002); however, this does not reject the possibility of a single saltation. Thus, a third possibility can be suggested: initial saltational increase of floral element number at the base of the clade with polymerous flowers [more precisely, dichotomous saltation by mutation(s) in *CLAVATA*-like gene(s)] with further radiation (including the origin of *T. calyptratus*) caused by unstable floral merism regulation in the modified genome. In this case, flowers of *S. subintegra* and *S. hemiepiphytica* should also be treated as fasciated. The idea of rapid changes in the genome structure at the base of this clade is congruent with the appearance of a calyptrate corolla in this group of species.

When falsifying saltation, it is recommended to 'describe as many features as possible' and treat separately the features that are potentially developmentally correlated (Bateman & DiMichele, 2002). Following this recommendation, we would have to consider many more than two major features (floral merism and calyptrate corolla) of *S. subintegra* and *T. calyptratus* because they should come apart in the merism of each whorl, calyx structure, floral symmetry, and a number of traits involved into calyptra formation. From this point of view, it is evident that the clade (*S. subintegra s.l.* + *S. hemiepiphytica*) + *T. calyptratus* represents a branch characterized by several morphological synapomorphies (Table 2). Such branches are supposed to be indicators of saltational evolutionary events. Consequently, if the saltational hypothesis is accepted, all the synapomorphies of the clade are regarded as results of a single mutation (Bateman & DiMichele, 2002). An important issue of this scenario is the need for understanding morphogenetic correlations between polymery (and unstable merism) of androecium and gynoecium and the loss of organ individuality in calyx and corolla, respectively. One could assume that the absence of positional information from discrete perianth organs could be an important factor of meristic instability. In addition, certain similarities between flower fasciation and complete congenital petal fusion can be found. Both phenomena include a loss (or partial loss) of individuality of ancestrally distinct structures (petals or flowers).

This case study of *S. subintegra* provides further morphological and phylogenetic evidence that con-

Table 2. Potential syn- and autapomorphies of *Tupidanthus calyptratus*, *Schefflera subintegra*, and *Schefflera hemiepiphytica*

Apomorphies	Comments
Potential synapomorphies of the clade comprising *Tupidanthus calyptratus*, *Schefflera subintegra*, and *Schefflera hemiepiphytica*	
1. Loss of sepal individuality	Among related taxa, recorded in *Schefflera actinophylla*
2. Loss of petal individuality	Not recorded in other members of the Asian *Schefflera* clade
3. Closure of the tube orifice by postgenital fusion of abaxial surfaces of opposite corolla parts and appearance of hairs of a special type covering the suture of postgenital closure	Not recorded in other members of the Asian *Schefflera* clade*
4. Stamens and carpels more than ten per flower (typically 15–25)	10- or 12-merous flowers are found in *S. actinophylla*
5. Stamen filaments straight (rather than incurved) in the flower bud	Not recorded in other members of the Asian *Schefflera* clade*
6. Stamens multitraced	Not recorded in other members of the Asian *Schefflera* clade*
7. Distinct scars of abscised stamens in postanthetic flowers and fruits	Not recorded in other members of the Asian *Schefflera* clade
8. Gynoecium disymmetry (or asymmetry) within both symplicate and synascidiate zones	Not recorded in other members of the Asian *Schefflera* clade
Potential autapomorphies of *T. calyptratus*	
1. Flowers disymmetric from inception	Not recorded in other Araliaceae
2. Stamens and carpels more than 50 per flower	Not recorded in other members of the Asian *Schefflera* clade
3. Lenticels and periderm on the inferior ovary wall	Not recorded in other Araliaceae
Potential synapomorphies of the clade comprising *S. subintegra* and *S. hemiepiphytica*	
None known	

*Characters not investigated in *S. hemiepiphytica* as a result of the absence of appropriate material.

firms the possibility of the saltation being involved in the origin of the highly polymerous flowers of *T. calyptratus*. Studies in genome structure and floral gene expression of *T. calyptratus* and its allies should represent the next step in checking this hypothesis.

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