Developmental floral morphology of Syngonium in the context of the tribe Caladieae (Araceae)

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Abstract

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The floral development of *Syngonium angustatum* is analysed in the context of a recently published molecular phylogeny of the *Araceae*. The initiation of discoid floral primordia occurs acropetally on the surface of the inflorescence. Female flowers, atypical bisexual flowers, sterile male flowers and male flowers are inserted on the same phyllotactic spirals on the spadix. Stamen primordia are initiated simultaneously on the periphery of more or less circular floral primordia. There are four stamens per flower (rarely three). In a synandrium, the fusion of stamens occurs very early during their developmental cycle. In some flowers one or two stamens remain free. The staminodes are also initiated on the periphery of the discoid floral primordium and their number varies from four to six. The growth of the fused staminodes will eventually form a longitudinal cavity in the centre of the mature synandrode. On the synandrodes located near the female zone, one or two staminodes remain free during development. No atypical bisexual flowers were observed on the inflorescence of *Syngonium*. The presence of a few calcium oxalate crystals was observed on the surface of all types of flowers. All the atypical flowers located at the base of the sterile zone corresponded to sterile male flowers and resulted from a more or less random disorganisation of the typical structure of a synandrode. In the *Aroideae,* free stamens or staminodes represent a plesiomorphic condition. The association of synandria and synandrodes is present in all early diverging genera of the tribe *Caladieae* and could represent the ancestral state. It is not clear if free stamens have evolved once or twice in the tribe *Caladieae,* both scenarios are possible.

Additional key words: aroids, inflorescence, phylogeny, oxalate crystals, flower

Introduction

The flowers of the *Araceae* represent a good model to study comparative floral development in relation to phylogeny. Recent molecular phylogenies published by Cabrera & al. (2008) and Cusimano & al. (2011) allow us to integrate floral developmental morphology in the context of a complete phylogenetic framework (Barabé 2013).

Aroideae are the biggest subfamily of the *Araceae* with 81 genera (Boyce & Croat 2011). They are generally characterised by unisexual flowers arranged in discrete zones on the spadix (Mayo & al. 1997). The female flowers are usually located in the lower portion of the inflorescence with male flowers (sterile and fertile) directly above them. Rare exceptions to this arrangement include *Calla* L., *Furtadoa* M. Hotta and *Spathicarpa* Hook. To date, species with unisexual flowers representing different genera have been investigated by a variety of authors from the perspective of floral anatomy or developmental morphology (e.g. Barabé & al. 2004a, 2008; Buzgó 1994; Barahona Carvajal 1977; Carvell 1989; Engler & Krause 1912; Eyde & al. 1967; French 1985; Fukai 2004; Hotta 1971; Mayo 1986, 1989; Uhlarz 1982, 1986).

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The developmental morphology of flowers has been well documented in genera where a sterile zone of flowers between the fertile male and the female zones is present (*Philodendron* Schott, *Schismatoglottis* Zoll. & Moritzi) or absent (*Culcasia* P. Beauv., *Cercestis* Schott). Atypical flowers with male and female characteristics are often found in the intermediate zone of aroid inflorescences and were referred as "monströse Blüten" by Engler & Krause (1912). To date, three different patterns of atypical bisexual flowers (ABFs) have been documented: the *Philodendron* type, the *Cercestis* type (Barabé & Lacroix 1999) and the *Schismatoglottis* type (Barabé & al. 2004c).

In the *Philodendron* type, ABFs generally consist of functional carpels and staminodes inserted on a single whorl. In the *Cercestis* type, ABFs are characterised by a functional or non-functional gynoecium surrounded by a few (1–5) vestigial stamens in a separate whorl (Barabé & Bertrand 1996: fig 30). In the *Schismatoglottis* type the intermediate zone located between the female and male zones consists of atypical flowers displaying a wide variety of forms ranging from more or less typical female flowers to functional male flowers (Barabé & al. 2004c), but with no residual ovary or stigma.

Floral development has been studied in different tribes of *Aroideae* (Barabé 2013). The genus *Syngonium* belongs to the *Dracunculus* clade sensu Cusimano & al. (2011), where it forms a monophyletic clade with its sister group, the genus *Caladium*. In tribe *Caladieae*, only the floral development of the genus *Caladium* has been studied (Barabé & Lacroix 2002). However, the early stages of development were not available and it was therefore not possible to describe the mode of formation of synandria and synandrodes in this genus. In this study, we document for the first time the initiation and development of synandria and synadrodes in the *Araceae*.

Syngonium is an interesting taxon from a morphological point of view, which can be used to infer the changes that may have taken place in developmental morphology during evolution. Even though observations on the thermogenesis of *Syngonium* have been published (Chouteau & al. 2007), there is no detailed information on its floral development. The analysis of floral development in *Syngonium* allows documentation of floral developmental morphology of *Caladieae* in the context of the recent molecular phylogenetic analysis by Cusimano & al (2011). In that respect, the clade comprising *Syngonium* and *Caladium* offers a phylogenetic and developmental framework to study the developmental process involved in closely related taxa. In the present study, we will assess whether the floral development of *Syngonium* can be integrated into the developmental patterns already recognised in the subfamily *Aroideae*.

The specific goals of this study are: (1) to document the mode of development of synandria and synandrodes in *Syngonium;* and (2) to compare the development of flowers of *Syngonium* and with other genera to further characterise the range of floral morphological features in the subfamily *Aroideae*.

Material and methods

Specimens of *Syngonium angustatum* Schott were collected in French Guiana (Montagnes de Kaw) in February 2011. A total of 25 inflorescences at various stages of development were fixed in formalin-acetic acid-alcohol (1 : 1 : 9 by volume) for a minimum of 24 hours and then stored in 70 % ethanol. Inflorescences were dissected under a stereo microscope to expose the surface of the spadix. The spadix was dehydrated in a graded ethanol series to absolute ethanol. Dissected inflorescences were dried in a LADD model 28 000 critical point dryer using CO_2 as a transitional fluid, mounted on metal stubs and gronded with conductive silver paint. Specimens were sputter coated 30 nm with gold/palladium using a Denton Vacuum Desk II sputter coater and viewed with a Cambridge S604 scanning electron microscope (SEM) with digital imaging capabilities (SEMICAPS®) (University of Prince Edward Island).

Results

Morphology of mature flowers and inflorescences

Syngonium angustatum Schott is a hemi-epiphyte that usually grows below the tree canopy. The inflorescences, generally 6–8 per sympodium, are situated in the upper portion of the plant (Fig. 1). The spadix (6–10 cm long) is whitish and about two thirds of the length of the spathe. The female flowers occupy the lower portion (1.3–2.6 cm) of the spadix (Fig. 1, 2), the male flowers its upper portion (2.5–6.5 cm) (Fig. 1, 3–4). Between those two zones there is a short intermediate zone (0.2–0.6 cm long) consisting of a few loosely packed sterile male flowers (Fig. 5). The green spathe (7–14 cm long) has a constriction zone corresponding to the intermediate zone on the spadix between the female and male flower zone (Fig. 1). The male zone represents approximately 65 % of the total length of the inflorescence, and the female zone 25 %.

Male flowers consist of 3–4 stamens united in a synandrium that is truncate apically (Fig. 3, 4). The anthers have a thick connective and open by pores located laterally on the thecae (Fig. 4). Even if stamens do not form a regular pattern on the surface of the inflorescence, it is possible to recognise individual male flowers on the spadix at dehiscence (Fig. 1). In *Syngonium angustatum* the surface of the epidermis of staminodes appears ± smooth.

Mature female flowers are oblong to oblong-obovoid and usually 2-locular. At maturity, they are exposed and more or less polygonal in top view (Fig. 2). The stigmas are discoid and raised on a short style (Fig. 2, 11).
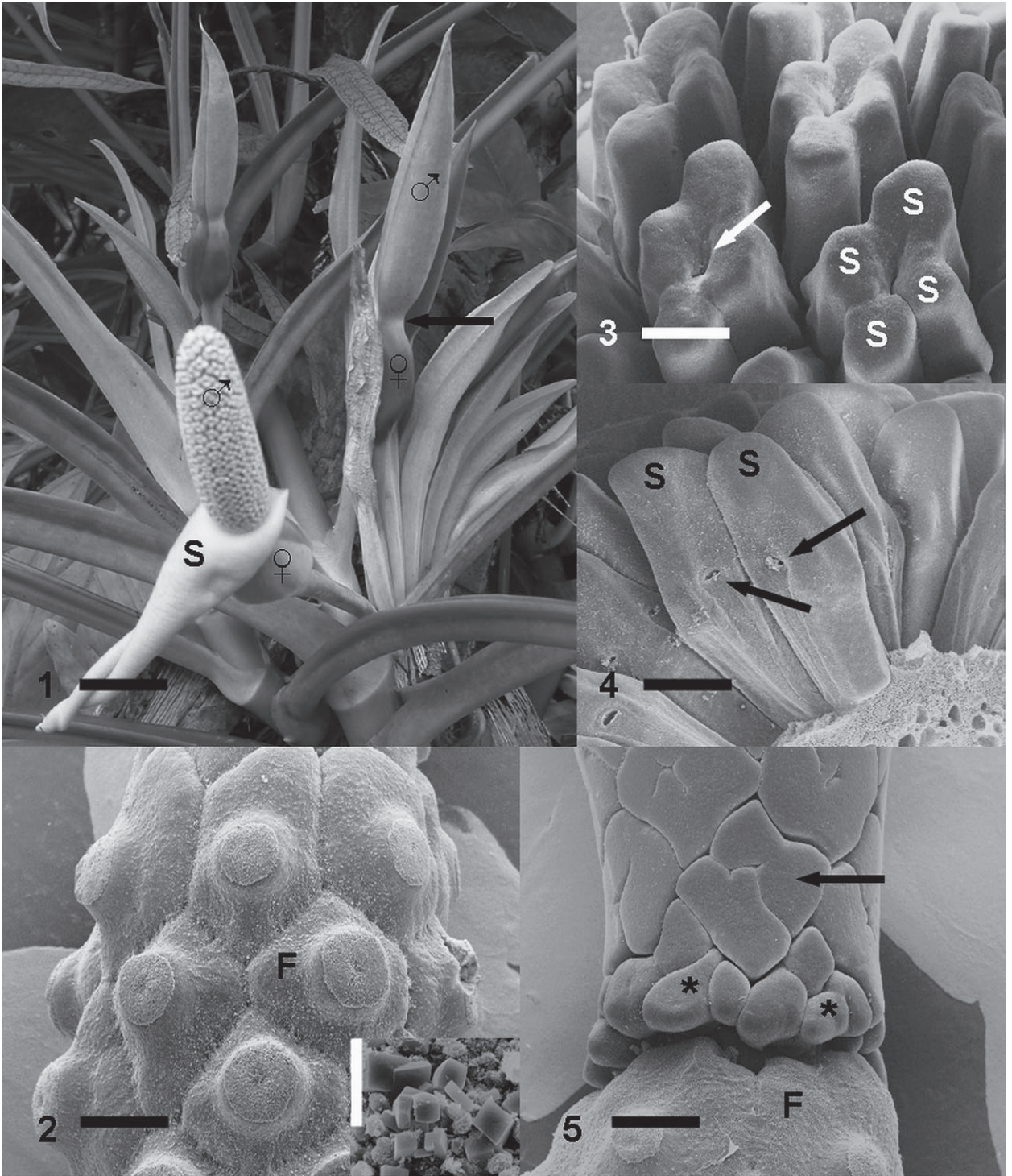
Fig. 1–5. *Syngonium angustatum*, features of mature inflorescences – 1: mature inflorescences in habitat showing female (♀) and male (♂) zones; S = spathe; arrow = constricted area of the spathe corresponding the intermediate zone of the inflorescence; 2: top view of female zone showing individual flowers (F); insert (with scale bar = 30 µm) shows extracellular calcium oxalate crystals on the surface of the female flowers; 3: top view of male flowers (synandria) consisting of 4 stamens (S); arrow = longitudinal cavity in the centre of a synandrium; 4: side view of synandria showing pores (arrows) on stamens (S); 5: intermediate zone of the inflorescence; arrow = complete synandrode, asterisks = partial synandrodes, F = female flower. – Scale bars: 1 = 2 cm, 2–5 = 750 µm.
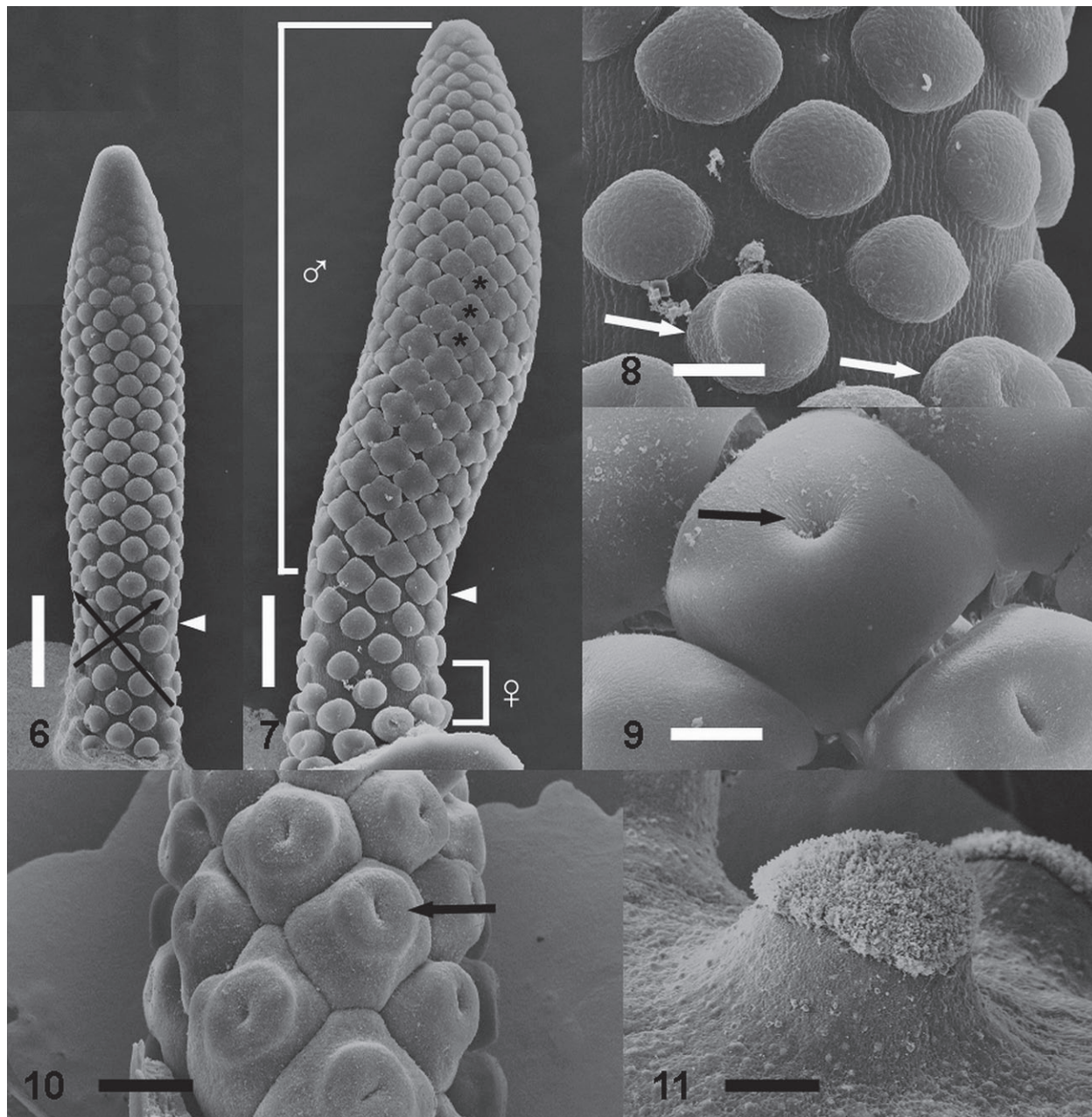
Fig. 6–11. *Syngonium angustatum,* early stages of development of the inflorescence and developmental morphology of the female flowers – 6: inflorescence showing the initiation of floral primordia arranged in parastichies (arrows); arrowhead = constricted area of inflorescence; 7: later stage of development of inflorescence showing the initiation of floral organs on male floral primordia (asterisks); ♂ = male zone, ♀ = female zone, arrowhead = intermediate zone and constricted portion of the inflorescence; 8: early stage of initiation of the female flowers showing the discoid shape of the basal part (arrows); 9: development of the wall surrounding the ovarian cavity (arrow); 10: early stage of formation of the stigmatic surface (arrow); 11: side view of the stigma on the mature flower. – Scale bars: 6–7 = 300 μm, 8 = 75 μm, 9 = 150 μm, 10–11 = 750 μm.

The presence of a few calcium oxalate crystals is observed on the surface of all types of flowers (Fig. 2, insert).

In the transition zone, appendages ranging from individual staminodes near the female zone to complete typical synandrodes at the base of the male zone are observed (Fig. 5).

Development

Development of the inflorescence — During early stages of development, the diameter of the inflorescence is more tapered above the female zone, at the level of the intermediate zone (Fig. 6, 7). The initiation of discoid floral primordia occurs acropetally (Fig. 6). The spadix, at the same stage, has an obcylindrical shape (Fig. 6, 7) and the
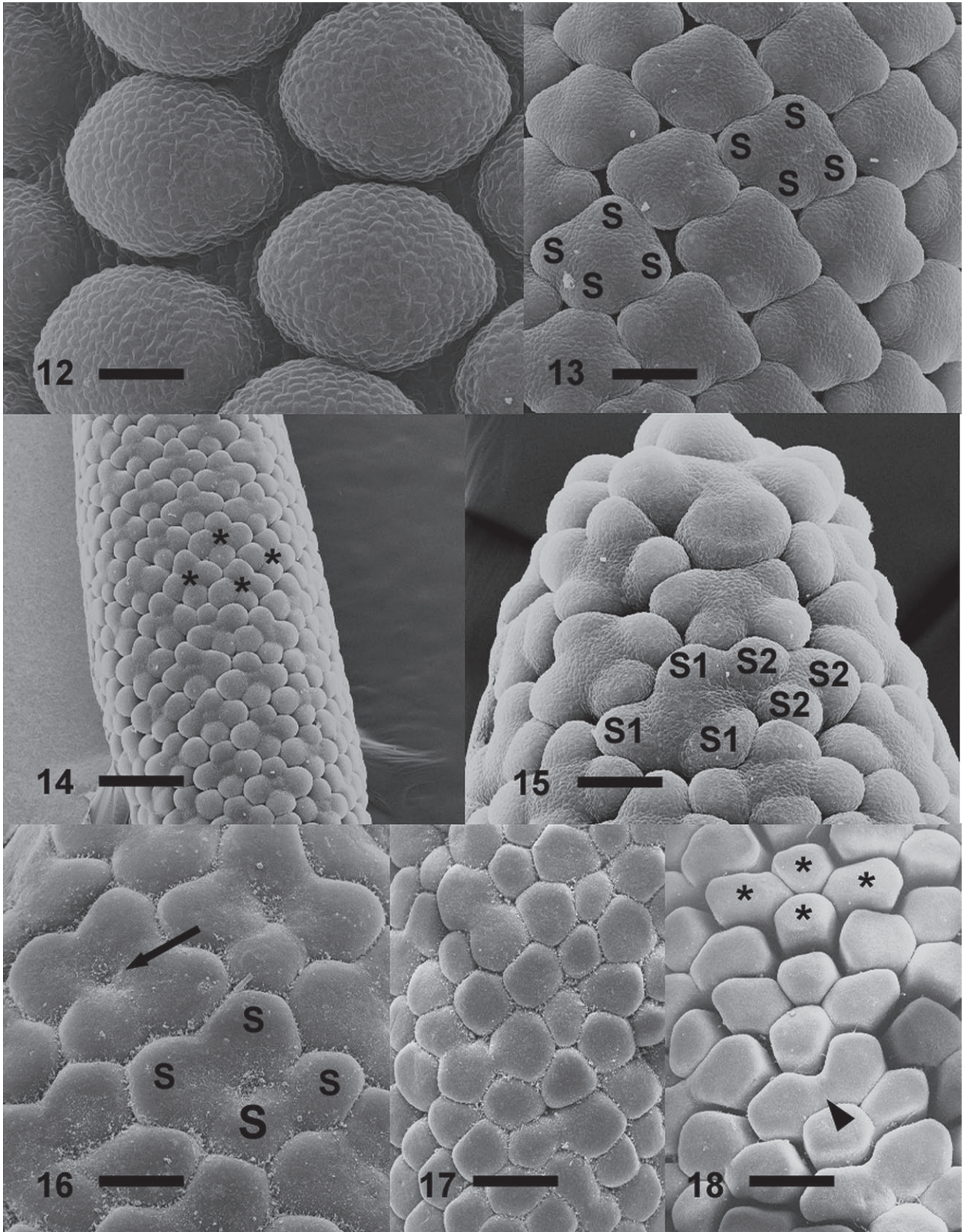
Fig. 12–18. *Syngonium angustatum,* development of male flowers – 12: male floral primordia prior to the initiation of stamens; 13: initiation of stamons (S) on male flowers; 14: later stage of stamen development in male zone; asterisks = central portion of male flowers surrounded by stamens; 15: fused floral primordia belonging to two different parastichies; S1 and S2 = stamens of fused flowers 1 and 2 respectively; 16: early stage of formation of the synandrium consisting of 4 stamens (S) and a central cavity (arrow); 17: later stage of development of male flowers where the central cavity is not distinguishable; 18: nearly mature synandria where fused (arrowhead) and free standing (asterisks) stamens are visible. – Scale bars: 12 = 30 µm, 13+15 = 75 µm, 14+16 = 300 µm, 17–18 = 750 µm.
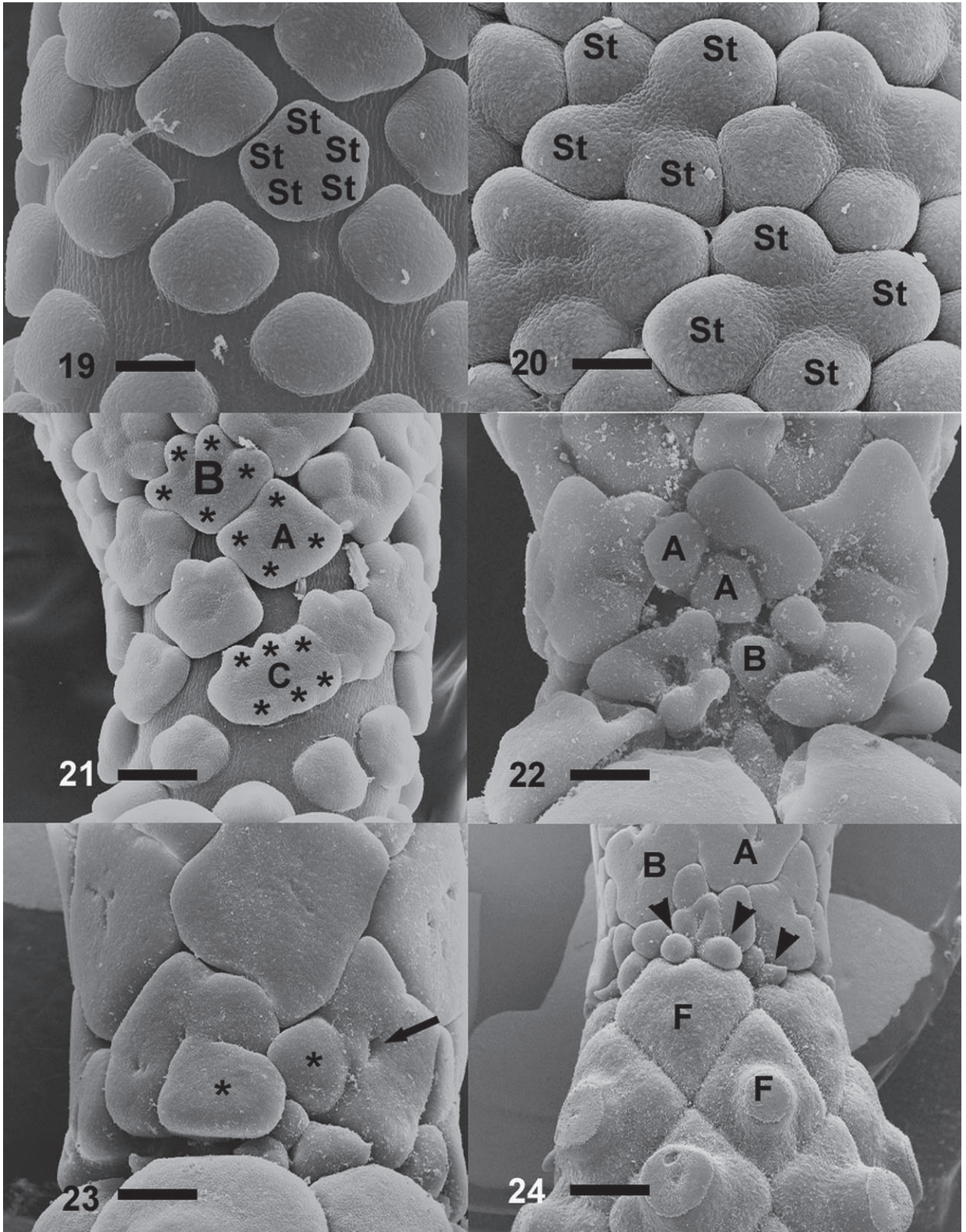
Fig. 19–24. *Syngonium angustatum,* developmental morphology of sterile male flowers – 19: early initiation of staminodes (St); 20: early stage of formation of synandrodes showing staminodial primordia (St); 21: examples of synandrodes consisting of 4 (A), 5 (B) and 6 (C) staminodes (asterisks); 22: constricted zone of inflorescence showing synandrodes with individual staminode primordia (A, B); 23: nearly mature segmented synandrode in the same zone as Fig. 22; asterisks = segments, arrow = longitudinal cavity in centre of synandrode; 24: transition zone showing typical synandrodes (A, B) and female flowers (F) flanking atypical structures (arrows). – Scale bars: 19–20 = 75 µm, 21–22 = 150 µm, 23 = 300 µm, 24 = 750 µm.

floral primordia form a more or less regular lattice pattern on the surface of the spadix, where distinct parastichies can be recognised (Fig. 6). At this point, there is no discontinuity in the phyllotactic pattern of the flowers across the different zones of the inflorescence. Female flowers, atypical flowers, sterile male flowers and male flowers are inserted on the same phyllotactic spirals in the lattice (Fig. 6).

When the spadix is approximately 2.5 mm long, the external morphology of the male and female flowers is more visible (Fig. 7). The development of flowers is acropetal along the entire length of the inflorescence. With the initiation of floral organs, male flowers acquire an irregular polygonal shape that becomes more accentuated during growth and packing of the flowers (Fig. 7). There is no terminal flower at the tip of the inflorescence.

Female flowers — During early stages of development, female floral primordia are hemispherical (Fig. 8), with the ovary inserted on a discoid base. The entire ovary wall is formed by the concrescence of the walls of adjacent carpels (Fig. 9). During later stages of development, the floral primordia come into contact with each other and eventually occupy all the available space between the flowers (Fig. 9, 10). The cavity visible in the centre of the ovary corresponds to the site where the style and discoid stigma eventually form (Fig. 9, 10, 11). A short stylar canal and a discoid stigma will develop from a rim of tissue above the ovarian cavity (Fig. 10, 11).

Male flowers — Stamen primordia are initiated simultaneously on the periphery of more or less circular floral primordia (Fig. 12, 13, 14). There are four stamens per flower (rarely three) and they are compactly arranged throughout development. During later stages of development, the floral primordia come in contact with each other. The size of the stamens increases and they eventually occupy all the available space between the flowers (Fig. 13, 14). Fusion of flowers belonging to two different parastichies can also be observed (Fig. 15). In a synandrium, the fusion of stamens occurs very early during their developmental cycle (Fig. 16) with the stamens united by their lateral sides (Fig. 4). This process leads to the formation of a longitudinal cavity in the centre of the flower that remains visible on mature flowers (Fig. 3). Although the flower of *Syngonium* is a synandrium, the stamens are not always all united. In some flowers one or two stamens remain free (Fig. 17, 18).

Synandrodes — The development of typical synandrodes is similar to that of synandria. However, the degree of fusion between staminodes is greater than that of stamens (Fig. 23). The staminodes are initiated on the periphery of the discoid floral primordium (Fig. 19) and their number varies from four (Fig. 20) to six (Fig. 21). During early stages of development, nearly all staminodes are united laterally (Fig. 20). The growth of the fused staminodes will eventually form a longitudinal cavity in the centre of the mature synandrode (Fig. 23).

Synandrodes located near the female zone also present some atypical features. One can observe incomplete synandrodes where one or two staminodes remain free during development (Fig. 22). Therefore, by the end of the developmental phase, more or less free staminodes are visible between the zone of synandrodes and the female zone (Fig. 24). The transition in floral morphology between the female zone and the male sterile zone is ± abrupt with no clearly recognisable zone of atypical bisexual flowers on mature inflorescences of *Syngonium* (Fig. 4, 24).

Discussion

Subfamily *Aroideae* is characterised by the presence of unisexual flowers, except for the genus *Calla* (Cusimano & al. 2011). However, in many genera, flowers with male and female organs are often found in the intermediate zone of the inflorescence, between the male and female zones (Barabé 2013). The atypical flowers located in the intermediate zone in *Syngonium* correspond to disorganised sterile male flowers that normally aggregate to form a synandrode. From a developmental point of view, these flowers may be considered as synandrodes consisting of a variable number of fused staminodes. However, in the genus *Syngonium* one does not find atypical bisexual flowers as in *Cercestis, Philodendron* and *Schismatoglottis.*

In *Syngonium,* as in *Caladium,* sterile male flowers are referred to as synandrodes. During early stages of development of the inflorescence, a few atypical synandrodes between the female zone and the male sterile zone are recognisable by their asymmetrical disorganised appearance. In *Caladium* few atypical flowers were also observed in the intermediate zone. Morphologically, these were interpreted as atypical bisexual flowers of the *Philodendron* type (Barabé & Lacroix 2002). However, in the inflorescence of *Syngonium* we did not observe any atypical bisexual flower. All the atypical flowers located at the base of the sterile zone corresponded to sterile male flowers and resulted from a more or less random disorganisation of the typical structure of a synandrode. This varying level of disorganisation is believed to be related to the proximity of the female zone, adjacent to the lower row of synandrodes. Contrary to the present study, the early stages of development of the atypical flowers were not available in *Caladium* and may necessitate a re-interpretation of atypical flowers in *Caladium.*

Unusual is the presence of a discoid basal portion on the female floral primordial (Fig. 8) similar to that seen in female flowers of *Culcasia* (Barabé & Bertrand 1996) and *Schismatoglottis* (Barabé & al. 2004c). However, this structure does not appear to have any phylogenetic significance.

Table 1. Characters of male, sterile and female flowers of genera belonging to the tribe *Caladieae* sensu Cusimano & al. (2011). The data are from Mayo & al. (1997).

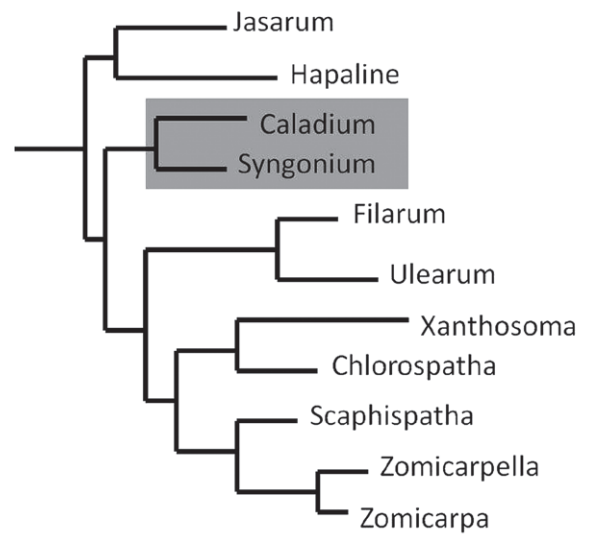| Genera	Stamens	Staminodes
Caladium	synandrium (3–5)	synandrode
Chlorospatha	synandrium (3–5)	free or synandrode (3–4)
Filarum	free	absent
Jasarum	synandrium (3–4)	synandrode
Hapaline	synandrium (3)	synandrode
Scaphispatha	synandrium (4)	free
Syngonium	synandrium (3–4)	synandrode
Ulearum	free	absent or present (free)
Xanthosoma	synandrium (4–6)	synandrode
Zomicarpa	free	absent or present (free)
Zomiocarpella	free	absent

Fig. 25. Phylogenetic position of the tribe *Caladieae* (shaded grey) revealed by Cusimano & al. (2011) in their molecular phylogeny of the *Araceae*.

The genus *Syngonium* forms a single clade with its sister group *Caladium* included in the tribe *Caladieae* (Cusimano & al. 2011), in which genera with and without staminodes exist (Table 1). However, neither of the two characters (synandrium and synandrode) characterise a monophyletic clade (Fig. 25). The association of synandria and synandrodes is present in all early diverging genera of the tribe *Caladieae* and could represent the plesiomorphic/ancestral state (Fig. 25). It is not clear whether free stamens have evolved once or twice in the tribe *Caladieae,* both scenarios are possible. With the exception of the genus *Scaphispatha,* the presence of a synandrium is always correlated with the presence of a synandrode; and on the other hand, free stamens are either associated with staminodes or not. Such associations might be explained by the fact that the determination of fused or free organs is early during floral development, and that same mechanism could apply to all flower primordia along the spadix axis.

Do the presence of synandria and synandrodes in *Aroideae* constitute a symplesiomorphic or an apomorphic character? In the *Aroideae,* male flowers forming synandria have arisen many times in different tribes or clades. However, it is only in *Spathicarpeae* that this character is a common feature of the tribe. During the development of synandria and synandrodes, we can recognise more or less free primordia during early stages of development. During subsequent stages of development, these primordia grow as a continuous ring to form a synandrium or a synandrode. Given that during early stages of development the primordia are free, this indicates that in the *Aroideae* free stamens or staminodes represent a plesiomorphic condition.

Developmental studies have shown that prismatic calcium oxalate crystals are visible on the surface of the apical portion of stamens of species of *Philodendron* (Barabé & al. 2004c) and *Schismatoglottis* (Barabé & al. 2004a), on the young appendices of *Arum* (Barabé & al. 2003) and on inflorescences of *Anthurium* (Barabé & Lacroix 2008). The accumulation of extracellular calcium oxalate crystals on the surface of stamens takes place before the release of pollen. This mode of release is similar to that observed in *Syngonium angustatum.*

In *Syngonium angustatum,* the crystals are produced on the surface of the epidermis during early stages of development, before anthers dehisce or the stigma forms. The production of prismatic crystals therefore appears to be morphologically independent from anther dehiscence. It is also possible that these crystals could remain enclosed in the spathe until the dispersal of pollen.

It is also plausible that in *Araceae,* as in other families, the extracellular oxalate crystals are a physiological consequence of the removal of calcium oxalate which may otherwise accumulate in toxic quantities in the plant (Franceschi & Horner 1980). The release of crystals could also depend on environmental conditions such as temperature, light intensity and water availability. A more detailed discussion on the development and role of extracellular calcium oxalate crystals can be found in Barabé & al. (2004b).

In conclusion, the structure of the atypical sterile male flowers of *Syngonium* shows that developmental constraints (genetic or physiological) experienced by the floral primordia in the intermediate zone are not exactly the same for all genera of *Aroideae*. The presence of different types of atypical flowers in *Aroideae* indicates that the mode of development of these particular structures is linked directly to morphogenesis of typical unisexual flowers, which represents a phylogenetic constraint canalising the nature or potential of atypical organs that can develop (Barabé 2013).

Acknowledgements

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