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FLORAL DEVELOPMENT AND PHYLOGENETIC POSITION OF *SCHISMATOGLOTTIS* (ARACEAE)

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In the inflorescence of *Schismatoglottis*, atypical sterile flowers are present between the male and female zones. Contrary to what occurs in *Cercestis* and *Philodendron*, where the atypical flowers are bisexual, in *Schismatoglottis* the atypical flowers consist of aberrant male or female flowers. These atypical unisexual flowers have different forms depending on their position in the inflorescence. The atypical flowers located near the male zone share characteristics with staminate flowers, and those located near the female zone have features in common with pistillate flowers. The developmental pathway of atypical flowers in *Schismatoglottis* is already channeled in the direction of female or male flowers before the appearance of aberrant appendages. Interpistillar sterile structures located in the female zone correspond to modified female flowers. The systematic position of *Schismatoglottis* is not fully resolved on a molecular phylogenetic analysis of 45 genera of Araceae, on the basis of chloroplast *trn*L intron and *trn*L-F intergenic spacer sequences. The floral ontogenetic pattern in *Schismatoglottis* represents a different pathway in the evolution of unisexual flowers in the subfamily Aroideae.

Keywords: floral development, molecular phylogeny, systematics, morphogenesis.

Introduction

Within the Araceae, the subfamily Aroideae, *sensu* Mayo et al. (1997), consists of 74 genera and is characterized by the presence of unisexual flowers. The female flowers are located in the lower portion of the spadix, and male flowers (sterile and fertile) are found above them. Several species with unisexual flowers representing a number of genera have been investigated by a variety of authors from the perspective of floral anatomy and developmental morphology (Engler and Krause 1912; Eckardt 1937; Eyde et al. 1967; Hotta 1971; Barahona Carvajal 1977; Uhlarz 1982, 1986; French 1985*a*, 1985*b*, 1986*a*, 1986*b*; Mayo 1986, 1989; Barabé and Forget 1988; Carvell 1989; Buzgó 1994, 2001; Boubes and Barabé 1997). Recently, Barabé and collaborators (Barabé and Bertrand 1996; Barabé and Lacroix 1999; Barabé et al. 2000) showed that the flowers of some genera of the Aroideae have many developmental features that could be analyzed at the ontogenetic and evolutionary levels (Barabé et al. 2002*a*).

Flowers with male and female characteristics (called "monströse Blüten" by Engler and Krause [1912, p. 16]) are often found in the intermediate zone of aroid inflorescences, between the male and female zones in genera with unisexual flowers. This phenomenon has been well documented in the genera *Cercestis* (Barabé and Bertrand 1996) and *Philodendron* (Boubes and Barabé 1996; Barabé and Lacroix 1999; Barabé et al. 2000). To date, two types of atypical bisexual flowers (ABFs) have been recognized: the *Philodendron* type and the *Cercestis* type (Barabé and Lacroix 1999). These two types seem to correspond to two different evolutionary trends (Barabé et al. 2002*a*). In the *Philodendron* type, ABFs generally consist of functional carpels and staminodes inserted on the same whorl. In the *Cercestis* type, the gynoecium and stamens are inserted on two different whorls. The ABFs are characterized by a functional or nonfunctional gynoecium surrounded by a few (one to five) vestigial stamens (Barabé and Bertrand 1996).

Until recently, few genera have been examined from a developmental perspective to determine the number of potential types of ABFs in the subfamily Aroideae. Even though a correlation between the types of ABFs and the phylogeny of the genera in the Aroideae has been established (Barabé et al. 2002*a*), a wider range of morphologies of atypical flowers in the subfamily Aroideae may be present. The developmental morphology of ABFs has been documented in genera with a sterile zone of male flowers between the typical male and female zones (*Philodendron*, *Caladium*) and in genera where such a zone is absent (*Culcasia*, *Cercestis*). However, no studies have examined what happens in taxa such as *Schismatoglottis*, where the sterile male zone is located above the male zone. The lack of floral developmental studies in the Araceae family results in part from the difficulty in obtaining enough material to adequately document the early stages of development (Barabé and Lacroix 2001). Recently, we were able to

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obtain sufficient material of *Schismatoglottis americana* A. M. E. Jonker & Jonker and *Schismatoglottis calyptrata* (Roxb.) Zoll. & Moritzi at different stages of development to extend our survey of the group.

In the inflorescence of *Schismatoglottis*, the morphological nature of the sterile organs is problematic. Hotta (1971) did not address this issue in his anatomical study of flowers of different genera of Araceae, which included *Schismatoglottis*. Although the floral morphology in different species of *Schismatoglottis* was described in detail in a recent thorough taxonomic study (Hay and Yuzammi 2000), an analysis of floral development is still lacking and is needed to determine the nature of the different types of sterile organs present on the inflorescence (Hay and Yuzammi 2000).

A molecular phylogenetic analysis of 33 genera of Araceae on the basis of the chloroplast *trn*L intron and *trn*L-F intergenic spacer sequences was recently published (Barabé et al. 2002*a*) and compared to available morphological data. We have built on this work by adding 12 new genera to the analysis, including *Schismatoglottis*. We use this new analysis and others published by French et al. (1995) and Mayo et al. (1997) to examine the distribution of the morphological types of atypical flowers in selected genera. More specifically, we will assess whether the different floral types appearing on the inflorescence of *Schismatoglottis* can be integrated in the phylogenetic pattern of the ABFs previously recognized in the subfamily Aroideae.

The specific goals of this study are (1) to compare the development of flowers of *Schismatoglottis* to other genera to further characterize the range of floral developmental morphologies in the subfamily Aroideae and (2) to determine the systematic position of the genus *Schismatoglottis* using a molecular phylogenetic analysis. From a general perspective, we are interested in finding out whether the distribution of the different types of flowers along the spadix acts as a constraint on the type of atypical flowers that can potentially develop. This analysis will focus on the developmental floral morphology and systematic position of *Schismatoglottis* to address this question.

Material and Methods

Developmental Study

Specimens of *Schismatoglottis americana* Zoll. & Moritzi were collected in French Guiana (Petit-Saut dam) in April 2002 (a voucher specimen, *Barabé 82*, is deposited at MT). Specimens of *Schismatoglottis calyptrata* (Roxb.) Zollinger & Moritzi were obtained from the living collection at the Montreal Botanical Garden (accession number 3152–59; *Barabé & Archambault 194*, MT).

A total of 14 inflorescences of *S. americana* and 16 inflorescences of *S. calyptrata* at various stages of development were fixed in FAA (1 : 1 : 9 by volume) and later transferred and stored in 70% ethanol. Inflorescences were dissected under a stereomicroscope to expose the spadix and were dehydrated in a graded ethanol series to absolute ethanol. Dissected inflorescences were then dried in a LADD model 28000 critical-point dryer using CO_2 as a transitional fluid, mounted on metal stubs, and grounded with conductive silver paint. Specimens were sputter-coated to ca. 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).

Molecular Phylogeny

Specimens used in the molecular analysis were collected in the field or taken from the living collection at the Montreal Botanical Garden (table 1). Methods for DNA extraction, amplification, and sequencing of *trn*L intron and *trn*L-F spacer are described by Barabé et al. (2002*a*).

Phylogenetic analyses were performed using PAUP*, version 4.0b3a (Swofford 2000). All characters were equally weighted and unordered, and insertion/deletion events were coded as separate presence/absence characters. Analyses were conducted with the heuristic search option and branch swapping performed using TBR (tree bisection and reconnection) and random addition sequence (1000 replicates). All optimal trees were kept in memory (MULPARS "on"), and branches with a minimum length of zero were collapsed. Branch support was calculated with bootstrap analyses using 1000 replicates and the "fast" stepwise addition option, as implemented in PAUP*.

Trees were rooted with *Acorus calamus*, which was also used by French et al. (1995) to root their tree. This facilitated comparison of our results with those of French et al. (1995). Although molecular analyses of the phylogeny of monocotyledons suggest that other families may be closer relatives of the Araceae (Duvall et al. 1993; Soltis et al. 2000), *Acorus* sequences are similar enough for accurate alignment.

Results

Morphology of Mature Flowers and Inflorescences

The mature inflorescence of *Schismatoglottis calyptrata* is divided into a lower female zone (50% of the total length), a middle male zone, and an upper appendix consisting of staminodes, the latter two representing ca. 25% of the total length of the inflorescence. In *Schismatoglottis americana*, all the male flowers are fertile, there is no appendix, and the female zone and the male zone occupy 20% and 40%, respectively, of the total length of the inflorescence. The male zone may be separated (*S. americana*) or not (*S. calyptrata*) from the female zone by a sterile portion (interstice). In *S. americana*, the interstice represents 40% of the length of the mature inflorescence.

In *S. americana* and *S. calyptrata*, the stamens are generally truncate and raised on short filaments (figs. 1*A*, 2*D*). In both species, the stamens do not form a regular pattern on the surface of the inflorescence, and it is consequently not possible to recognize what might be termed male flowers in mature inflorescences (fig. 1*A*).

In *S. americana*, the narrow connective is flat. Each theca has two pollen sacs that open through a common pore located at the margin of the stamen (fig. 1*A*). In *S. calyptrata*, the stamens are partially connate in small groups of two or three (fig. 2*D*, 2*E*). The pollen sacs open through large, apical, slitlike pores. The anthers are dumbbell shaped, with apically depressed thecae (fig. 2*D*, 2*E*).

In *S. americana*, the epidermis of stamens is characterized by pegged and ridged cells, giving the surface of stamens a rough texture appearance (fig. 1*B*). In *S. calyptrata*, this characteristic is less apparent, and the surface of the epidermis appears more or less smooth (fig. 2*B*, 2*C*).

In *S. calyptrata*, the staminodes are irregularly polygonal and flat. The top surface of the staminodes is covered with many depressions and stomata (fig. 2*A*). In *S. americana*, there are no staminodes above the male zone.

In *S. americana*, the presence of a few calcium oxalate crystals mixed with pollen was observed (fig. 1*C*). In *S. calyptrata*, the connective forms a slight dome and is covered by a mass of extracellular calcium oxalate crystals (fig. 2*E*, 2*F*). The oxalate packages are produced in the center of the upper surface of the stamen (fig. 2*E*, arrow). The release of oxalate packages occurs when the stamen and the stigma are fully mature. These exudates form globular masses on the surface of the epidermis. During early stages of development, the calcium oxalate package appears to be covered by the cuticle, and the growth of the oxalate package eventually breaks through that cuticular cover (fig. 2*E*, 2*F*). No crystalline formations are visible on the surface of the apical portion of nearly mature stamens in *S. americana*.

The pistils are exposed and more or less cylindrical in *S. americana* (fig. 1*D*), whereas in *S. calyptrata*, they are globular (fig. 2*G*). The stigmas are discoid in both species, sessile in *S. americana* (fig. 1*D*), and raised on a short style in *S. calyptrata* (fig. 2*I*). Irregularily shaped interpistillar sterile structures are often found among pistils in *S. calyptrata*. They are apically narrow, clavate, and taller than the pistils (fig. 2*H*, 2*I*). In *S. americana*, interpistillar sterile structures are absent. In the transition zone, single appendages ranging in form from atypical pistils to atypical stamens are observed (described in greater detail in “Development”) (fig. 1*E*; fig. 5*A*, 5*B*; fig. 7*A*–7*G*).

Development

Inflorescence. During early stages of development of *S. americana*, the diameter of the inflorescence is more tapered above the female zone, at the level of the transition zone (fig. 1*E*). The male floral primordia are inserted without apparent order on the surface of the inflorescence (fig. 1*E*). However, parastichies of female flowers are recognizable (fig. 1*E*; fig. 3*D*–3*H*). When spadices of *S. americana* are ca. 5 mm long, the distinct external morphology of the male, female, and atypical flowers is visible (fig. 1*E*). During the development of the inflorescence of *S. americana*, the length of the interstice (transition zone) will increase considerably. At the developmental stage represented in figure 1*E*, this zone represents ca. 5% of the total length of the inflorescence. However, in mature inflorescences this proportion increases to 40%.

Staminate flowers. The number of stamens per flower is very difficult to determine in these species. However, on the basis of the position of pores that are peripheral (fig. 1*A*), we can estimate that it ranges from two to four. In *S. americana*, the stamens form prominent protuberances early in their development (fig. 3*A*) and are compactly arranged throughout development (fig. 3*B*, 3*C*). During later stages of development, the location of each of the pollen sacs is visible (fig. 3*B*), and the location of dehiscence pores also becomes recognizable (fig. 3*C*). On young inflorescences of *S. calyptrata*, one can easily recognize the thecae of the stamens (fig. 4*D*) with their characteristic dumbbell shape (fig. 4*E*). During the growth of the stamens, the connective will become slightly elevated above the thecae (fig. 4*C*, 4*E*).

Pistillate flowers. During early stages of development of *S. americana*, female floral primordia have a hemispherical shape, and the concrescent carpel primordia are initiated on the periphery of the floral primordia (fig. 3*D*). At this stage, two to four cavities are visible at the base of the ovaries, each cavity representing one carpel (fig. 3*D*, arrows). The entire ovary wall is formed by the concrescence of the walls of adjacent carpels (fig. 3*E*, 3*F*). During later stages of development, the floral primordia come into contact with each other, and, like stamens, they will eventually occupy all the available space between flowers (fig. 3*F*, 3*G*). The cavity that is visible in the center of the ovary corresponds to the site where the discoid stigma (fig. 3*G*) eventually forms (fig. 3*H*).

In *S. calyptrata*, the ovary has a triangular or tetragonal shape (fig. 4*F*). The ovary is topped by a rim of tissue (fig. 4*G*) from which a short stylar canal and a discoid stigma will develop (fig. 2*I*). The clavate interpistillar staminodes are found at irregular intervals between the female flowers. We found it impossible to recognize a particular pattern in the distribution of staminodes in the female zone. At the base of the female zone, interpistillar staminodes and underdeveloped female flowers can be observed (fig. 4*G*).

Sterile male flowers. In *S. calyptrata*, the top portion of the young columnar staminodes has an irregular shape. A depression (fig. 4*A*) can also be observed in the center of the staminode. During the growth of the inflorescence, the number of depressions or small cavities increases (fig. 4*B*). The staminodes will eventually occupy all the available space between flowers and will form a network of irregular polygons on the surface of the inflorescence (fig. 4*B*, 4*C*).

Atypical flowers. In *S. americana*, the intermediate zone located between the female zone and the male zone consists of atypical flowers, the morphological nature of which is very difficult to determine (fig. 5*A*, 5*B*). These flowers display a wide variety of forms ranging from more or less typical female flowers (fig. 5*A*) to atypical male flowers (fig. 6*A*). There is also a gradient in the morphology of the atypical flowers. The atypical flowers located near the female zone have more pistillate characteristics than those located near the male zone, which resemble staminate flowers. During early stages of development, the atypical flowers of the intermediate zone are located close to one another (fig. 1*E*). The elongation of the intermediate zone results in widely interspersed flowers (fig. 5*A*, 5*B*).

The atypical flowers located near the female flowers are flattened and have a structure that resembles a rudimentary stigma (fig. 5*A*). During early stages of development, the stigmatic cavity of many atypical flowers is reduced or absent (fig. 5*B*). The atypical flowers located in the median part of the intermediate zone (fig. 5*A*, arrows) are completely flattened and elongated. They consist of two parts: a triangular elongated basal part, and an obovate flattened upper portion.

Table 1

Species Examined for the Phylogenetic Analysis, with Collection Locality and Voucher Information

Taxa	Collection	Voucher	GenBank accession no.
True Araceae group (*sensu* Mayo et al. 1997):			
Subfamily Aroideae (flowers unisexual, except for ABFs):			
Aglaonema crispum (Pitcher & Manda) D. H. Nicolson	JBM (24–76)	Barabé & Archambault 198	AY555179
Aglaonema modestum Schott ex Engl.	JBM (6969–38)	Barabé & Chantha 86	AY054700
Alocasia odora (Roxb.) C. Koch	JBM (4974–39)	Barabé & Chantha 93	AY054705
Ambrosina bassii L.	Corsica	Barabé 180	AY555185
Amorphophallus paeoniifolius (Dennst.) Nicolson var. *campanulatus* (Decne.) Sivadasan	JBM (3397–88)	Barabé & Chantha 98	AY054703
Amorphophallus titanum Becc.	JBM (853–1999)	Barabé & Archambault 199	AY555180
Anchomanes difformis (Blume) Engl.	JBM (3991–84)	Barabé & Archambault 191	AY555186
Anubias barteri Schott var. *caladiifolia* Engl.	JBM (1648–86)	Barabé & Chantha 90	AY054710
Anubias heterophylla Engl.	JBM (1909–99)	Barabé & Archambault 197	AY555168
Arisaema sp. Mart.	JBM (s.n.)	Barabé 150	AY054704
Arisarum vulgare Targ.-Tozz.	JBM (2944–01)	Barabé 178	AY555181
Arum italicum Mill.	France	Barabé 181	AY555183
Arum pictum L.f.	Corsica	Barabé 179	AY555182
Caladium bicolor (Ait.) Vent.	JBM (1590–95)	Barabé & Chantha 96	AY054708
Cercestis stigmaticus N. E. Br.	JBM (4088–84)	Barabé &Archambault 192	AY555170
Colocasia esculenta (L.) Schott	JBM (1511–00)	Barabé & Archambault 176	AY555184
Cryptocoryne balansae Gagnep.	. . .	Barabé & Archambault 203	AY555173
Culcasia saxatilis A. Chev.	JBM (4094–84)	Barabé & Chantha 91	AY054713
Culcasia mannii Engl.	JBM (1938–99)	Barabé & Archambault 196	AY555169
Dieffenbachia pittieri Engl. & Krause	JBM (1633–53)	Barabé & Chantha 88	AY054714
Gonatopus angustus N. E. Br.	JBM (4106–84)	Barabé & Turcotte 101	AY555167
Homalomena rubescens (Roxb.) Kunth	JBM (1721–55)	Barabé & Turcotte 108	AY054723
Philodendron sp. Schott	Biodôme (7208–92)	Barabé & Archambault 184	AY555166
Montrichardia arborescens (L.) Schott	French Guiana	Barabé 54	AY054716
Nephthytis afzelii Schott	JBM (4175–84)	Barabé & Chantha 95	AY054702
Peltandra virginica Kunth	JBM (2501–82)	Barabé 152	AY054707
Philodendron ornatum Schott	French Guiana	Barabé 30	AY555165
Philodendron billietiae Croat	French Guiana	Barabé 36	AY054721
Philodendron callosum K. Krause	French Guiana	Barabé 68	AY555163
Philodendron fragantissimum (Hooker) Kunth	French Guiana	Barabé 44	AY054717
Philodendron insigne Schott	French Guiana	Barabé 39	AY054718
Philodendron linnaei Kunth	French Guiana	Barabé 76	AY555164
Philodendron melinonii Brongn. ex Regel	JBM (2246–86)	Barabé & Chantha 85	AY054719
Philodendron solimoesense A.C. Smith	French Guiana	Barabé 42	AY054720
Philodendron rudgeanum Schott	French Guiana	Barabé 37	AY054722
Pistia stratiotes L.	JBM (2627–93)	Barabé 153	AY054706
Rhektophyllum mirabile N. E. Brown	JBM (3568–85)	Barabé & Chantha 89	AY054712
Schismatoglottis americana Jonker & Jonker	French Guiana	Barabé 82	AY555171
Schismatoglottis calyptrata (Roxb.) Zoll. & Moritzi	JBM (3152–59)	Barabé & Archambault 194	AY555172
Spathicarpa sagittifolia Schott	JBM (1936–53)	Barabé & Turcotte 104	AY054715
Syngonium auritum (L.) Schott	Biodôme (732–92)	Barabé & Archambault 190	AY555177
Syngonium podophyllum Schott	JBM (3046–1959)	Barabé & Archambault 200	AY555178
Syngonium triphyllum Birdsey ex T. B. Croat	JBM (3404–88)	Barabé 97	AY555176
Xanthosoma sp. Schott	JBM (2250–86)	Barabé & Turcotte 107	AY054709
Xanthosoma sagittifolium L. Schott	JBM (189–1959)	Barabé & Archambault 195	AY555175
Zamioculcas zamiifolia (Lodd.) Engl.	JBM (7324–39)	Barabé & Chantha 84	AY054725
Subfamily Calloideae (flowers bisexual):			
Calla palustris L.	JBM (3519–40)	Barabé & Archambault 174	AY555174
Subfamily Lasioideae (flowers bisexual):			
Anaphyllopsis americana (Engl.) A. Hay	French Guiana	Barabé 83	AY054726
Dracontium polyphyllum L.	French Guiana	Barabé 50	AY054727
Subfamily Pothoideae (flowers bisexual):			
Anthurium consobrinum Schott	Biodôme (7226)	Barabé & Archambault 183	AY555155
Anthurium jenmanii Engl.	JBM (3554–87)	Barabé & Chantha 92	AY054730
Anthurium guildingii Schott	JBM (2436–92)	Barabé & Lavoie 156	AY054729
Pothos scandens L.	JBM (2690–54)	Barabé & Lavoie 157	AY054731

Table 1

(*Continued*)

Taxa	Collection	Voucher	GenBank accession no.
Subfamily Monsteroideae (flowers bisexual):			
Amydrium magnificum (Engl.) Nicolson	JBM (3399–88)	Barabé & Chantha 99	AY054735
Amydrium medium (Zoll. & Moritzi) Nicolson	JBM (2977–59)	Barabé & Archambault 186	AY555161
Amydrium medium (Zoll. & Mor.) Nicolson	JBM (4104–84)	Barabé & Archambault 201	AY555160
Epipremnum falcifolium Engl.	JBM (2287–54)	Barabé & Turcotte 100	AY054732
Heteropsis sp. Kunth	French Guiana	Barabé, Forest & Gibernau 147	AY054739
Holochlamys beccarii Engl.	JBM (4107–84)	Barabé & Turcotte 103	AY555157
Monstera deliciosa Liebm.	JBM 4884–39	Barabé & Lavoie 158	AY054733
Monstera adansonii var. *klotzschiana* (Schott) Madison	JBM (2263–86)	Barabé & Chantha 94	AY054734
Monstera adansonii var. *klotzschiana* (Schott) Madison	JBM (2424–92)	Barabé & Archambault 187	AY555162
Rhaphidophora africana N. E. Br.	JBM (3990–84)	Barabé &Turcotte 110	AY054736
Rhodospatha sp. Poepp. & Endl.	JBM (2086–00)	Barabé & Archambault 193	AY555156
Spathiphyllum floribundum N. E. Br.	JBM (265–89)	Barabé & Archambault 188	AY555159
Spathiphyllum patinii (R. Hogg) N. E. Br.	Biodôme (7001–2000)	Barabé & Archambault 189	AY555158
Spathiphyllum wallisii Hort.	JBM (2471–54)	Barabé & Turcotte 105	AY054738
Stenospermation popayanense Schott	JBM 1875–55	Barabé & Lavoie 159	AY054737
Proto-Araceae group (*sensu* Mayo et al. 1997):			
Orontioideae (flowers bisexual):			
Lysichiton camtschatcense (L.) Schott	JBM (932–49)	Barabé 153	AY054740
Orontium aquaticum L.	JBM (1989–91)	Barabé & Archambault 177	AY555154
Symplocarpus feotidus (L.) Nutt.	JBM (55–52)	Barabé 154	AY054741
Acoraceae:			
Acorus calamus L.	JBM s.n.	Joly 226	AY054741

Note. All voucher specimens are deposited at MT. *Trn*L intron and *trn*L-F intergenic spacer sequences are deposited in GenBank.

There is no discernable stigmatic structure or ovarian cavity on these flowers (fig. 5*A*, arrows). The atypical flowers are often clustered in groups of two (fig. 5*A*), three (fig. 5*A*, 5*B*), or, rarely, four (fig. 6*A*).

The atypical flowers located near the male zone also present a great diversity of forms. For example, the structure in figure 6*A* consists of four appendages that look like aberrant or atypical stamens, each consisting of a flat filament and two underdeveloped thecae. In a similar structure (fig. 6*B*), which appears to be a group of three underdeveloped stamens, the epidermal tissue of the ventral surface is disorganized. Flattened atypical flowers with a cavity (depression) at the base of the appendage were also often observed (fig. 6*C*). The epidermal surface of this cavity looks like that of the three-part structure in figure 6*B*. There appears to be a gradient, from the base to the apex of the transition zone, from typical female flowers (fig. 6*H*), aberrant female flowers, tri-clustered atypical flowers, three- or four-clustered atypical male flowers to typical stamens.

Many atypical and normal female flowers consist of a short ovary on top of a discoid base (fig. 6*F*, arrow; fig. 6*G*, 6*H*), a structure that is not present in male flowers. Examples of two particular atypical flowers can be observed (fig. 6*G*). Structure A appears to be a combination of an atypical flower with an underdeveloped ovary and a flower with an aborted ovary. The presence of a discoid base is also visible. Structure B (fig. 6*G*) consists of four appendages representing a gradient in their structure and position. The two appendages located near the male zone (1 and 2) are elongated, flattened, and without female characteristics. They look like the stamens located above them. However, appendages 3 and 4, located near the female zone, are smaller, globular shaped, and resemble aborted ovaries. Although appendage 3 can also be interpreted as an aborted stamen, appendage 4 looks like an incomplete gynoecium or carpel primarily because of its horseshoe shape (arrow). There is also a gradient in the expression of morphological features of atypical flowers ranging from flowers consisting of a reduced ovary (*O*) and a well-defined basal part to atypical flowers consisting of a portion with no appendages on the side of the female zone and a portion with stamen primordia (*St*) on the side of the male zone (fig. 6*H*).

The intermediate zone of *S. calyptrata* also presents a morphological gradient in the atypical flowers, ranging from typical female flowers to typical male flowers (fig. 7*A*). However, the types of atypical flowers in this species are different from those previously described in *S. americana*. Atypical flowers located above typical female flowers are generally flattened; some of them have a prominent cavity in the center, with a residual stigmatic structure (fig. 7*A*, flower 1; fig. 7*B*, arrow). Floral structure 2 (fig. 7*A*) represents another morphological variant. It is a flattened, triangular structure also topped with a residual stigma. Other atypical flowers (fig. 7*A*, flowers 3, 4, 5) located near the male zone have a clavate form and resemble what we refer to as "interpistillar pistillodes." Their morphological identity is unclear. Near the male zone, there are usually a few atypical flowers with two different appendages united at their base (fig. 7*C*). In figure 7*C*, one of these appendages looks like an interpistillar staminode (*Pd?*) and the other like a stamen (*St?*).

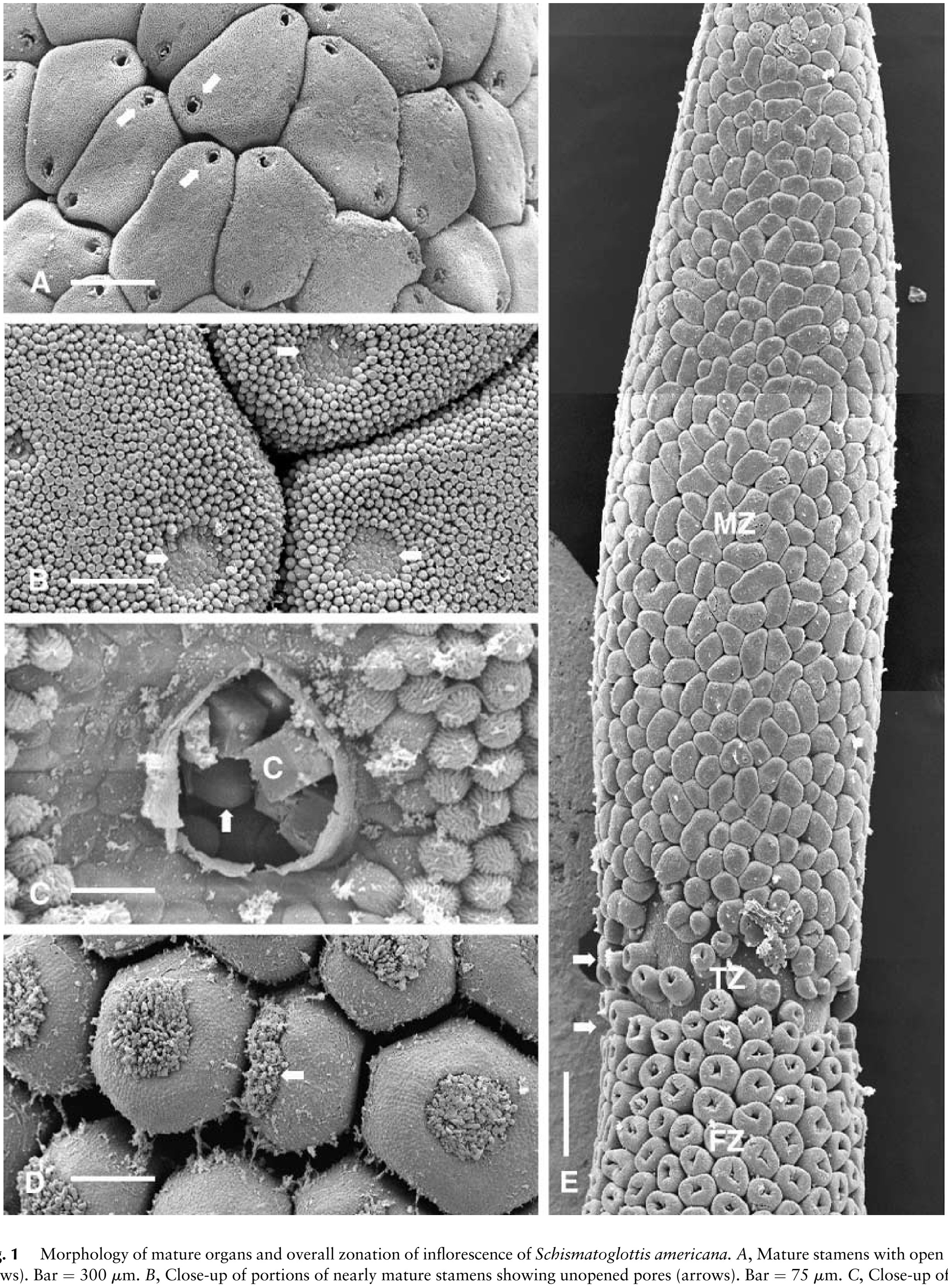

Fig. 1 Morphology of mature organs and overall zonation of inflorescence of *Schismatoglottis americana*. *A*, Mature stamens with open pores (arrows). Bar = 300 μm. *B*, Close-up of portions of nearly mature stamens showing unopened pores (arrows). Bar = 75 μm. *C*, Close-up of pore showing pollen grains (arrow) and crystals (*C*). Bar = 15 μm. *D*, General view of mature female flowers. Note the presence of a partially formed female flower with half a stigmatic surface (arrow). Bar = 300 μm. *E*, General view of inflorescence at an early stage of development. *FZ* = female zone; *TZ* = transition zone between male and female zone (boundaries denoted by arrows); *MZ* = male zone. Bar = 300 μm.

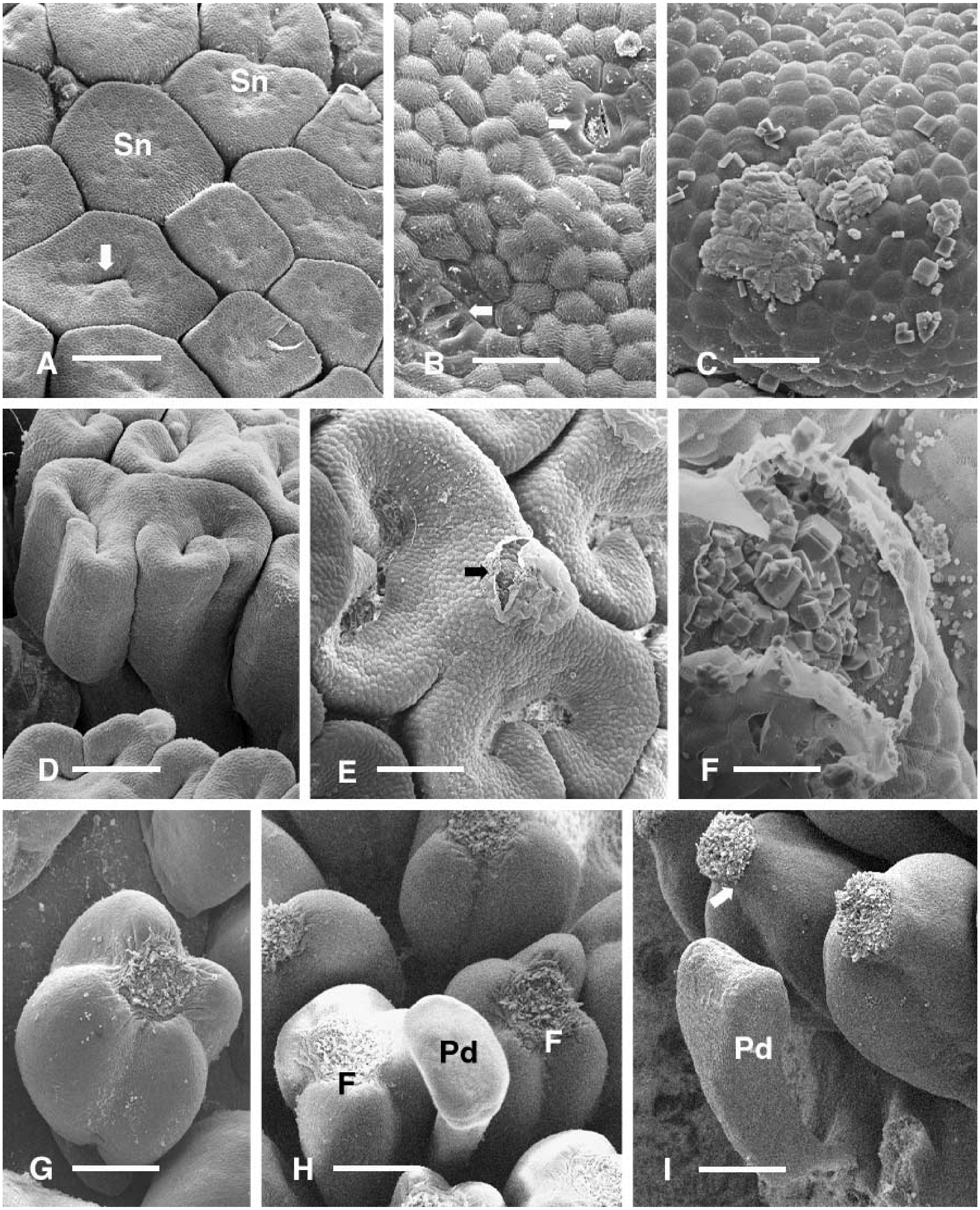

Fig. 2 Morphology of mature organs of the inflorescence of *Schismatoglottis calyptrata*. *A*, Top view of staminodes (*Sn*) surface. Arrow = depression. Bar = 300 μm. *B*, Close-up of stomata (arrows) on the top surface of staminodes. Bar = 30 μm. *C*, Close-up of calcium oxalate crystals. Bar = 30 μm. *D*, General view of a stamen. Bar = 300 μm. *E*, Top view of stamens showing crystals (arrow) in the middle portion. Bar = 150 μm. *F*, Exposed oxalate crystals through a break in the cuticle. Bar = 30 μm. *G*, General view of female flower. Bar = 300 μm. *H*, Pistillode (*Pd*) between two female flowers (*F*). Bar = 150 μm. *I*, Pistillode (*Pd*) located at the base of the female zone. Bar = 300 μm.

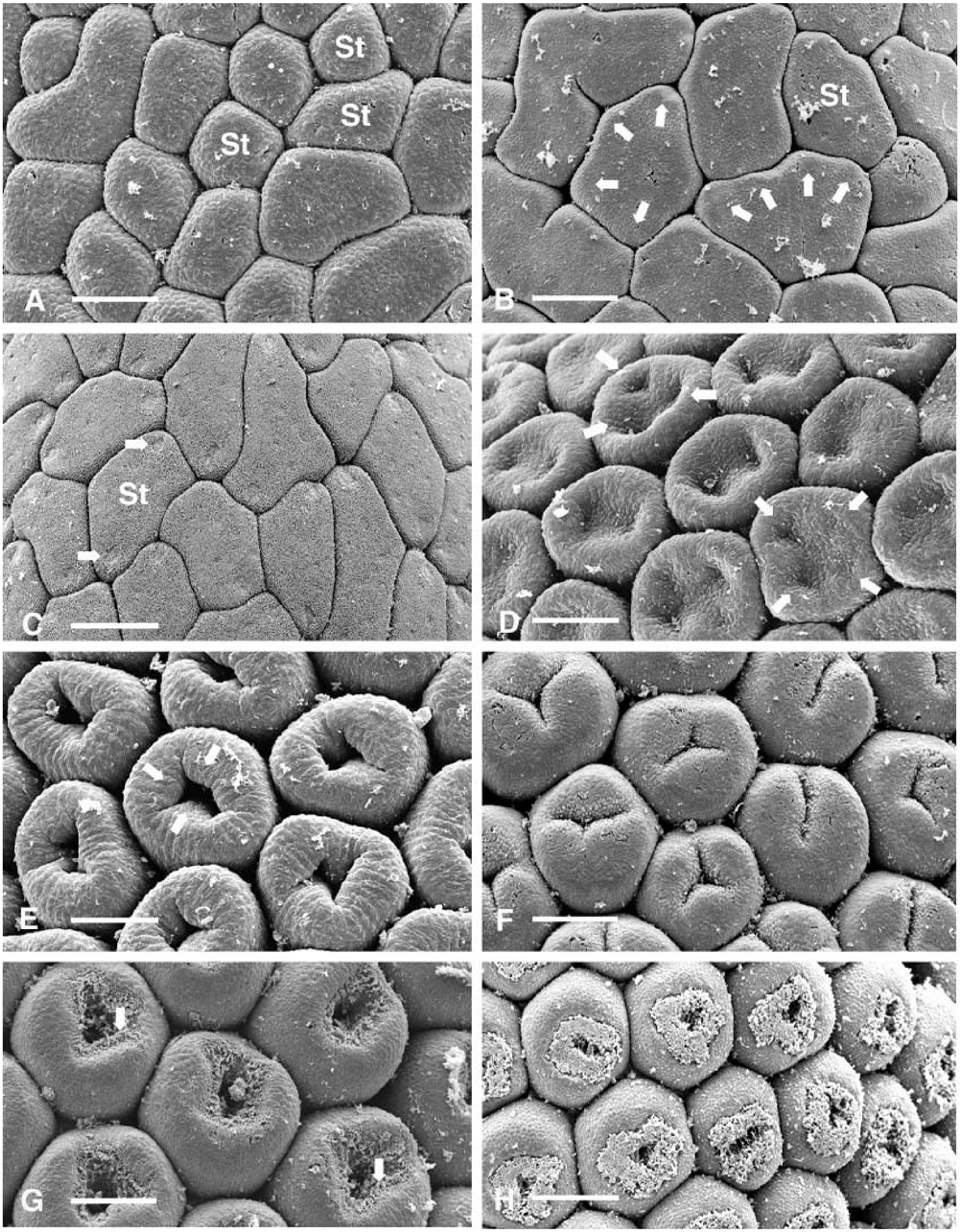

Fig. 3 Stages of development of male and female flowers in *Schismatoglottis americana*. *A*, Stamens (*St*) at an early stage of formation. Bar = 75 μm. *B*, Stamens (*St*) prior to the appearance of pores. Contour of pollen sacs are visible (arrows). Bar = 150 μm. *C*, Nearly mature stamens (*St*) prior to the opening of pores (arrows). Bar = 300 μm. *D*, Early stage of carpel initiation (arrows) on female flowers. Bar = 75 μm. *E*, Growth of ovary wall around locules (arrows). Bar = 75 μm. *F*, Stage at which the ovary closes in. Bar = 150 μm. *G*, Top view of flowers showing an early stage of formation of the stigmatic surface (arrows). Bar = 150 μm. *H*, Nearly mature flowers with stigmatic surface. Bar = 150 μm.

Clusters of two typical stamens were frequently observed near the zone of pistillate flowers (fig. 7*D*).

During early stages of development (fig. 7*E*), there is an acropetally progressive reduction in the size of female flowers located near the interpistillar pistillode (*Pd*). Figure 7*E* shows a continuous transition between typical female flowers (*F*) and typical staminate flowers.

Some atypical flowers have very aberrant morphologies. Figures 7*F* and 7*G* show a diversity of forms ranging from typical female flowers (*F*) to typical stamens (*St*). A more or less typical clavate pistillate flower (*B*), inserted between two undefined structures (A and C) is shown in figure 7*F*. The atypical structure A is flat and has no recognizable invagination, in comparison with bifid structure C. The presence of such structures indicates the reciprocal influence of male and female zones of the inflorescence. During early stages of development, the flattened atypical flowers with a stigmatic crest have a bifid apical portion that looks like a pair of lips (fig. 7*G*).

Phylogenetic Analysis

The final matrix consists of 72 sequences, representing 45 aroid genera and *Acorus calamus*. Excluding the alignment-ambiguous regions (782 bp), the matrix consists of 1153 nucleotide positions and 32 insertion or deletion events coded as binary presence/absence characters. Among these, 458 characters are variable, of which 281 are potentially phylogenetically informative and 177 characters are unique to particular sequences (autapomorphic).

The phylogenetic analysis produced 24 most parsimonious trees of 846 steps, with a consistency index (CI) of 0.607 and retention index (RI) of 0.828. The strict consensus tree is shown in figure 8, with bootstrap values above 50% indicated above branches. All subfamilies recognized by Mayo et al. (1997), namely Orontoideae, Monsteroideae, Pothoideae, and Lasioideae, are supported as monophyletic, with strong bootstrap support (99%, 97%, 95%, and 100%, respectively) (fig. 8).

In this analysis, subfamily Aroideae *sensu* Mayo et al. (1997) is supported as monophyletic, except that the genus *Calla* is embedded within it and the *Zamioculcas-Gonatopus* clade occurs in an unresolved position at its base. The position of subfamily Lasioideae (*Anaphyllopsis-Daracontium*) also is not resolved relative to that of the Aroideae. Our phylogenetic analysis does not support the subfamilies Calloideae and Aroideae in the sense of Grayum (1990).

Discussion

Atypical Flowers

Hay and Yuzammi (2000) state that in the genus *Schismatoglottis*, the intermediate zone located between male and female flowers (interstice) generally consists of staminodes. However, as these authors noted, this zone may also be absent (*Schismatoglottis wallichii*) or occupied by apparently abortive pistils (e.g., *Schismatoglottis elegans*), interpistillar staminodes and sterile anthers (*Schismatoglottis scortechinii*), interpistillar staminodes and scattered groups of smaller staminodes (*Schismatoglottis rupestris*), or staminodes that resemble those of the appendix (*Schismatoglottis zonata*). This indicates the wide range in type of appendages that can develop in the intermediate zone. In *Schismatoglottis americana* and *Schismatoglottis calyptrata*, the intermediate zone of the inflorescence also exhibits many atypical flowers displaying a wide variety of forms.

In *S. americana*, the atypical flowers have a basal discoid portion similar to that seen in female flowers of *Culcasia* and *Cercestis* (Barabé and Bertrand 1996). However, in contrast to *Cercestis* and *Philodendron*, ABFs with rudimentary or fully developed organs of both sexes were not observed. The atypical flowers present in the interstice do not correspond to any type of atypical flowers that have been analyzed previously (Barabé et al. 2002*a*).

In *S. americana* and *S. calyptrata*, there is a gradual transition between typical female flowers and stamens. In the upper portion of the intermediate zone, the atypical flowers look like aborted stamens, and in the lower portion, the atypical flowers are similar in appearance to underdeveloped female flowers (fig. 7*A*). In the upper portion of the female zone, there is also a row of female floral primordia that are poorly developed in comparison with those located directly below (fig. 7*G*). The basal cavity present on some flattened atypical flowers (fig. 6*C*) can be interpreted as a residual ovary. In addition, many atypical flowers are topped with a small or residual stigma (figs. 6*E*, 7*A*). From the upper portion of the female zone on the inflorescence to the base of the male zone, the ovarian characteristics on individual flowers disappear more or less completely and are progressively replaced by the androecium (fig. 7*A*). On the basis of the morphological structure of the floral forms intermediate between typical female and male flowers, one may conclude that a single stamen corresponds, from a morphological point of view, to a pistil.

Even though the structures are clustered in groups of two or three, each element corresponds to a single atypical flower. Each stamen constitutes a single flower. Consequently, when stamens are partially connate into small groups of two (fig. 7*D*), we can interpret this as a mass of male flowers in which there is a tendency for local connation of filaments. Hay and Yuzammi (2000, p. 13) reflect this point of view by noting "the absence of functional and weak structural individuation of groups of floral parts in this genus." However, these authors do not provide any morphological interpretation of the nature of the stamens. On the basis of the above interpretation, the atypical structure represented in figure 7*C* would correspond to the union of a staminode and a pistillode. However, it is not possible to determine whether this ABF corresponds to the *Cercestis* type or the *Philodendron* type (Barabé et al. 2002*a*).

The morphological nature of interpistillar sterile structures, which are interpreted as staminodes by Hay and Yuzammi (2000), is very difficult to determine. For example, in *Schismatoglottis lingua* (Hay and Yuzammi 2000, fig. 15), the interpistillar sterile structures look like underdeveloped stamens; they consist of an elongated structure resembling a filament and a globose upper part that looks like an aborted anther. Conversely, in *Schismatoglottis wahaiana* (Hay and Yuzammi 2000, fig. 18), the interpistillar sterile structures have a clavate form and look like underdeveloped

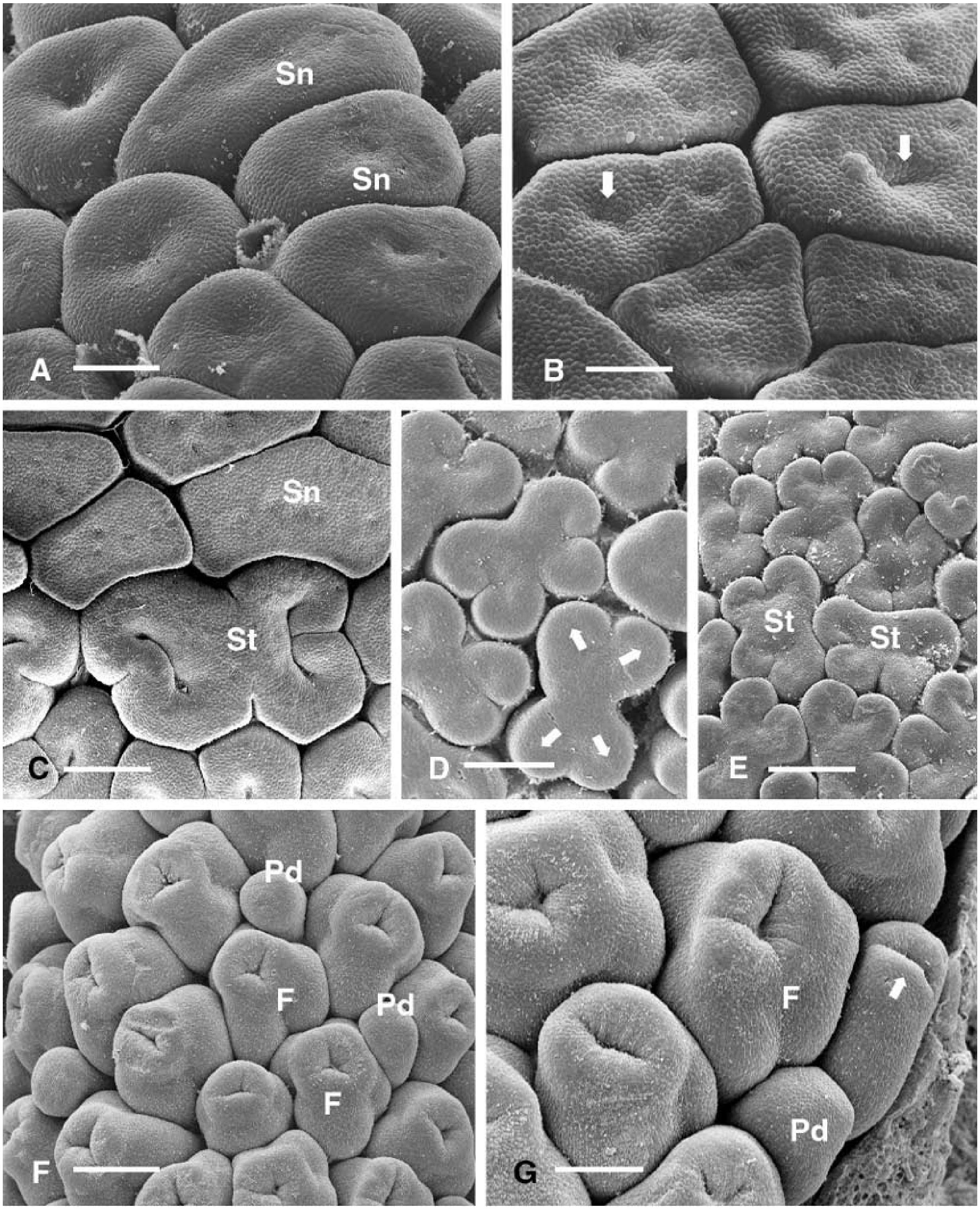

Fig. 4 Stages of development of sterile male, male, and female flowers of *Schismatoglottis calyptrata*. *A*, Early stage of formation of staminodes (*Sn*). Note central depression on structures. Bar = 150 μm. *B*, Later stage of development showing uneven surface of staminodes. Depressions (arrows) are still visible at this stage. Bar = 150 μm. *C*, Nearly mature staminodes (*Sn*) near adjoining zone of stamens (*St*). Bar = 300 μm. *D*, Top view of stamens with visible pollen sacs (arrow). Bar = 200 μm. *E*, Crowding of stamens (*St*) at a later stage of development. Bar = 300 μm. *F*, Portion of female zone showing pistillodes (*Pd*) and female flowers (*F*). Bar = 300 μm. *G*, Nearly mature pistillodes (*Pd*) and female flowers (*F*) in the basal portion of the female zone. Note the presence of an aborted female flower (arrow). Bar = 150 μm.

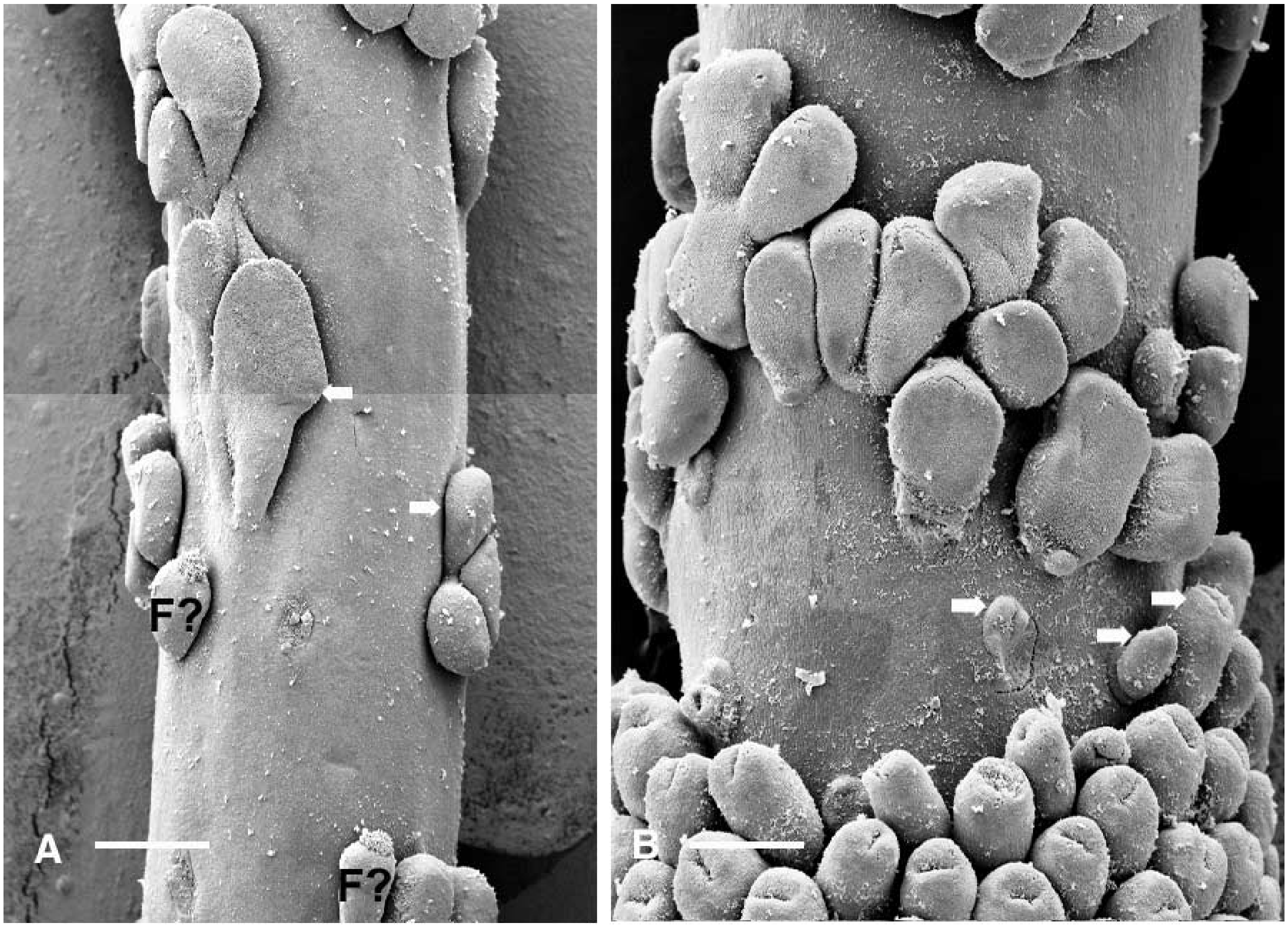

Fig. 5 General view of the transition zone during early stages of development of the inflorescence of *Schismatoglottis americana*. *A*, Flattened pistillodes (arrows) are interspersed along the inflorescence axis. Bar = 750 μm. *B*, Variation in pistillode shape in the transition zone (central portion of image). Bar = 300 μm. Arrows = atypical flowers.

female flowers. In *S. calyptrata*, the interpistillar pistillodes located at the base of the female zone also look like underdeveloped female flowers. Structures intermediate in morphology between typical female flowers and pistillodes are also observed (fig. 6*G*). On the basis of these results and a morphological comparison between species, we can conclude that interpistillar sterile structures correspond to modified female flowers, or pistillodes.

The presence of atypical flowers is probably related to the existence of a morphogenetic gradient between typical female flowers and male flowers (Barabé and Lacroix 2000). During early stages of development, when the length of the interstice is very short, the presence of atypical flowers in the genus *Schismatoglottis* is believed to be the result of a developmental constraint (physiological) exerted by the female zone on the lower side of the inflorescence and by the male zone on the upper side. The hypothesis of a hormonal gradient was formulated to explain the presence of ABFs in the inflorescences of both *Philodendron* (Barabé and Lacroix 2000; Barabé et al. 2000) and *Cercestis* (Barabé and Bertrand 1996). On the basis of this interpretation, it is plausible to think that atypical flowers are subjected to the simultaneous influence of male and female flowers along a hormonal gradient. However, in contrast to what happens in *Cercestis* and *Philodendron*, where ABFs develop instead of unisexual flowers, the flowers located in the intermediate zone in the inflorescence of *Schismatoglottis* never escape the developmental constraints of unisexuality.

Extracellular Calcium Oxalate Crystals

Extracellular crystal deposition is a characteristic feature of many gymnosperm species (Oladale 1982; Fink 1991*a*; Pennisi et al. 2001). In angiosperms, the presence of extracellular calcium oxalate crystals has been reported for Casuarinaceae (Berg 1994), *Gleditsia* (Borchert 1984), *Nymphaea* (Franceschi and Horner 1980; Kuo-Huang 1992), *Dracaena* (Fink 1991*b*), and *Sempervivum* (Fink 1991*b*; Vladimirova 1996; Pennisi et al. 2001). In a recent survey of distribution of calcium oxalate crystals in monocotyledons, there is no mention of extracellular crystals in this group of plants (Prychid and Rudall 2000). D'Arcy et al. (1996) reported the presence of calcium oxalate crystals (referred to as oxalate packages) mixed with pollen in some members of Araceae, such as *Anthurium*, *Calla*, and *Zantesdechia*. Recent developmental

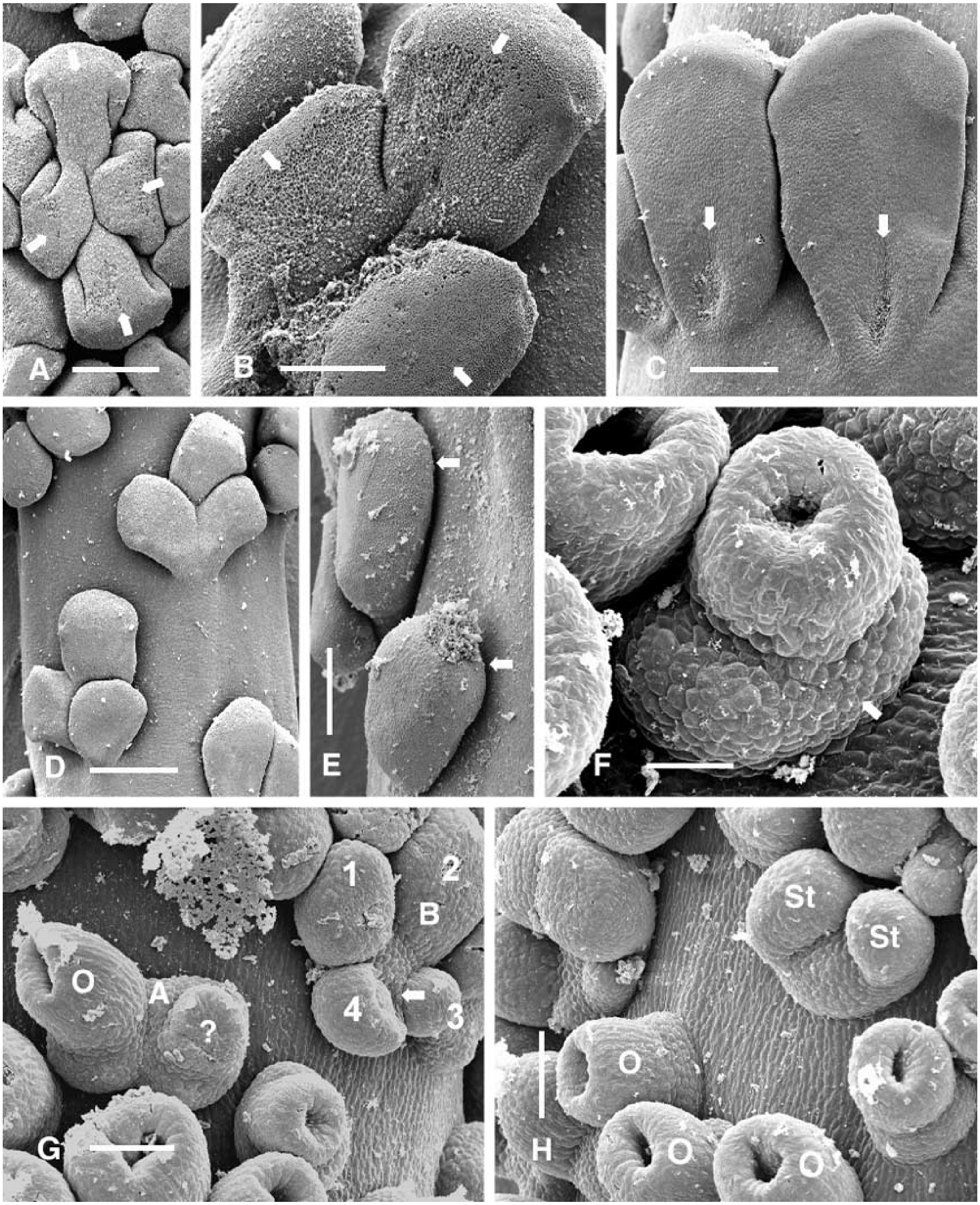

Fig. 6 Variations in floral types in the transition zone of the inflorescence of *Schismatoglottis americana*. *A*, Group of four abnormally shaped stamens (arrows). Bar = 750 μm. *B*, Group of three floral organs (arrows). Bar = 300 μm. *C*, Floral organs with visible depressions at their base (arrows). Bar = 300 μm. *D*, Trimerous groupings of floral organs in the transition zone. Bar = 750 μm. *E*, Female flowers (arrows) with a flattened appearance in the transition zone. Bar = 300 μm. *F*, Female flowers with a swollen basal portion (arrow). Bar = 30 μm. *G*, Group of floral organs labeled *A* consists of an ovary-like portion (O) and undifferentiated primordium (?). Group of floral organs labeled *B* consists of four undefined primordia, one of which resembles an opened carpel (arrow). Bar = 75 μm. *H*, Variety of floral morphologies in the transition zone ranging from ovary (O) to stamens (*St*). Bar = 75 μm.

studies have shown that extracellular calcium oxalate crystals are visible on the surface of the apical portion of nearly mature stamens of many species of *Philodendron*. These exudates form a globular mass on the surface of the epidermis (Barabé and Lacroix 2001; Barabé et al. 2002*b*). However, in *Philodendron*, the oxalate packages are not observed on the mature stamens after the opening of the spathe. In contrast, in *S. calyptrata*, the accumulation of extracellular calcium oxalate crystals also occurs when the stamens are mature and the stigmatic surface receptive (fig. 2).

There is evidence to indicate that in Araceae extracellular oxalate crystals play a biotic role in inhibiting herbivory (Franceschi and Horner 1980) or enhancing pollination (D'Arcy et al. 1996). In species where extracellular crystals are produced during anther dehiscence (e.g., *Schismatoglottis*), oxalate crystals could be related to pollination by providing a visual signal or a scent interesting to insects (D'Arcy et al. 1996).

Phylogeny and Developmental Morphology

With few exceptions, these new results based on *trn*L intron and *trn*L-F spacer sequences corroborate those of French et al. (1995) on the basis of chloroplast DNA restriction site data, as well as our previous study (Barabé et al. 2002*a*). There is also no notable difference between our results and those of Cho and Palmer (1999), who recently published a molecular phylogenetic analysis of 14 aroid genera based on the mitochondrial *cox1* gene. The major clades identified in our analysis correspond to those recognized by Cabrera et al. (2003): Orontioideae, Pothoideae, Monsteroideae, Lasioideae, and Aroideae. As in the analyses of Cabrera et al. (2003), the Calloideae (Calla) are embedded within the Aroideae.

Relative to our previous analysis (Barabé et al. 2002*a*), the position of *Anubias* is not resolved (fig. 8). In this new analysis, the genus *Rhektophyllum*, which is included in the genus *Cercestis* by Mayo et al. (1997), appears as the sister group of *Cercestis* (fig. 8). This differs from the result obtained by Barabé et al. (2002*a*), which, due to an error during the preparation of samples, led us to erroneously conclude that *Rhektophyllum* was the sister group of *Anchomanes*. The genera *Anchomanes* and *Nephthytis* are sister taxa, and they form a clade with the genus *Aglaonema* (fig. 8).

The genera *Arisarum* and *Ambrosina*, which were not included in our previous analysis (Barabé et al. 2002*a*), occur in the same clade, with the genus *Peltandra* as sister group. The genus *Arum* appears in the same clade as *Pistia*, *Colocasia*, *Arisaema*, and *Alocasia*, and this clade in turn is sister to a group that includes *Peltandra*, *Arisaema*, and *Alocasia* (fig. 8). This is in accordance with the results of French et al. (1995) but differs from those of Mayo et al. (1997). In the analysis of Mayo et al. (1997), *Peltandra* occurs in a clade that contains 14 genera, which include *Alocasia*, *Colocasia*, *Caladium*, *Syngonium*, and *Xanthosoma*.

The genera *Schismatoglottis* and *Cryptocoryne* form a monophyletic group, except that the genus *Schismatoglottis* is not supported as monophyletic. The close relationships of these two genera is supported in the analysis of French et al. (1995), where the tribe Cryptocoryneae and Shismatoglottideae occur together in a monophyletic group. However, in our analysis, the phylogenetic position of the *Schismatoglottis*-*Cryptocoryne* clade is unresolved. In the cladogram of French et al. (1995), the tribe Schismatoglottidae (clade V, fig. 8) represents a lineage distinct from other members of the Aroideae.

The *Cercestis* type of ABFs occurs in the genera *Cercestis*, *Culcasia*, *Dieffenbachia*, *Spathicarpa*, and in the perigonate genus *Zamioculcas* (fig. 8). To date, the *Philodendron* floral type has been observed only in the genera *Caladium*, *Philodendron*, and *Montrichardia* (Barabé et al. 2002*a*). However, the presence of atypical flowers of a different type in the inflorescence of *Schismatoglottis* indicates that the range of types of atypical flowers present in the Aroideae is greater than previously described.

As a group, clades I, II, and III (fig. 8) consist of genera characterized by the presence of ABFs of the *Cercestis* type (clade III) and *Philodendron* type (clade I and II). The presence of ABFs of the *Cercestis* type in two clades (*Gonatopus*-*Zamioculcas* and clade III) that do not form a monophyletic group clearly indicates that this character has evolved at least twice. However, given the lack of resolution among clades of Aroideae and absence of developmental data for numerous genera, it is not possible to determine whether the *Philodendron* type of ABFs correspond to a synapomorphy within the Aroideae. If we base our interpretation of the evolution of atypical flowers on the cladogram of Mayo et al. (1997), which is more resolved, we come to the conclusion that neither the *Philodendron* nor the *Cercestis* type of ABFs constitute synapomorphies.

Since the phylogenetic position of the *Schismatoglottis*-*Cryptocoryne* clade is not resolved, it is difficult to compare the type of atypical flower of *Schismatoglottis* with the phylogenetic distribution of other types of atypical flowers in genera for which information was available (fig. 8). Given that the atypical flowers of *Schismatoglottis* do not correspond to the *Cercestis* type or the *Philodendron* type, we consider that these represent a different pathway in the evolution of unisexual flowers in the subfamily Aroideae and that they are a new type of atypical flower.

In the genus *Schismatoglottis*, as in *Cercestis* and *Culcasia*, the atypical floral primordia are inserted on a discoid base (fig. 6*F*). Such a structure does not exist in the genus Philodendron. This indicates that the atypical flowers of *Schismatoglottis* are more closely related to the *Cercestis* type than to the *Philodendron* type. However, an unusual flower (fig. 6*G*, flower *B*) consisting of four undefined primordia, one of which ressembles an open carpel, is observed in *S. americana*, indicating a possible transformation similar to that of the *Philodendron* type. Since the phylogenetic position of the *Schismatoglottis*-*Cryptocoryne* clade (V) is not resolved (fig. 8), developmental and phylogenetic studies of related genera are needed to determine whether the atypical flowers of *Schismatoglottis* are more closely related to the *Cercestis* type or to the *Philodendron* type.

In conclusion, our study shows that the atypical structures that are present in the intermediate zone of the inflorescence of a number of taxa of Aroideae differ morphologically and phylogenetically from one another. On the basis of available data, the correlation between phylogenetic analyses and the morphological nature of atypical flowers is not perfect at the family or subfamily level. A more detailed investigation of

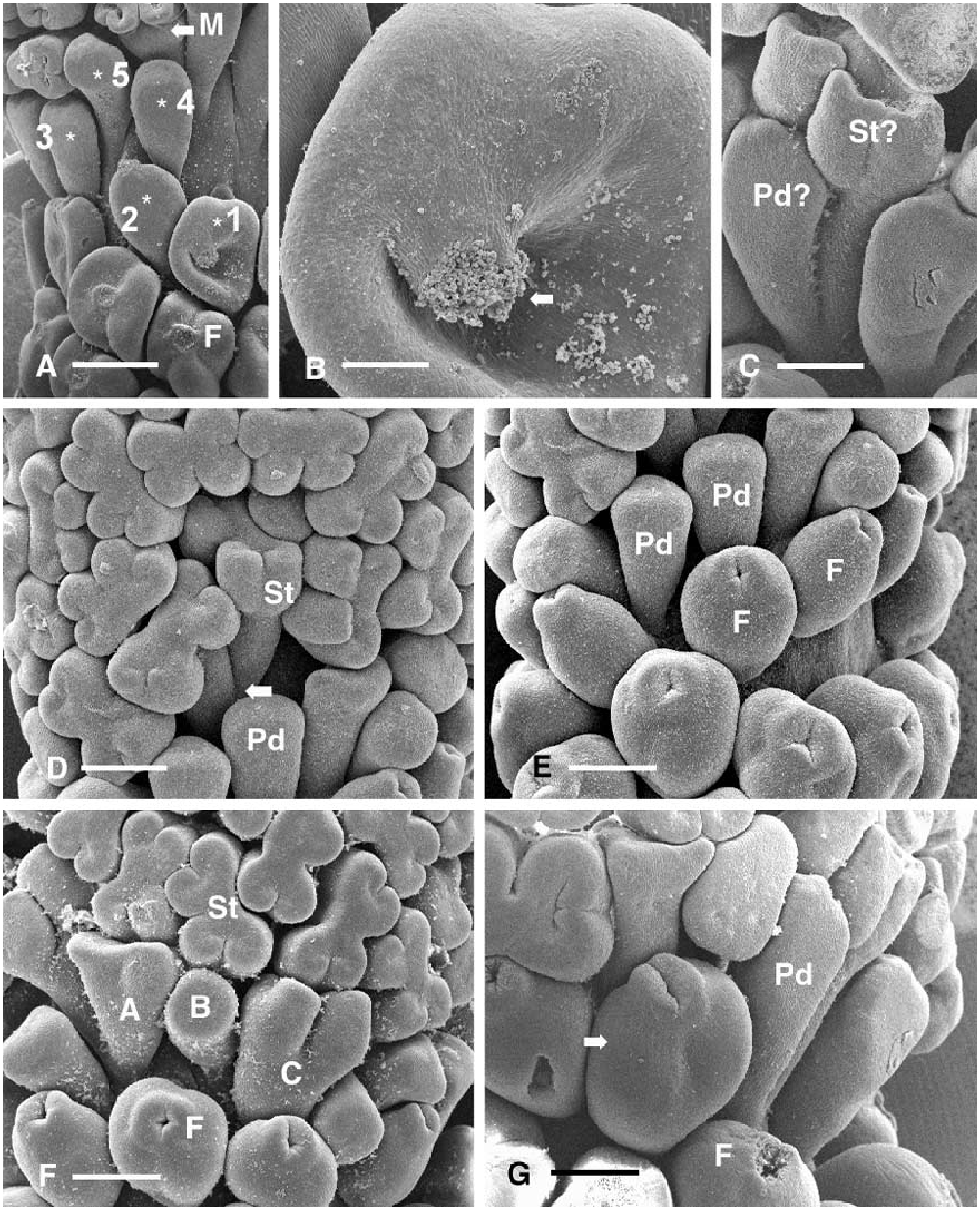

Fig. 7 Variety of morphologies in the transition zone in inflorescences of *Schismatoglottis calyptrata*. *A*, General view of the transition zone showing organs (*) intermediate between typical female flowers (*F*) and male flowers (*M*). Bar = 750 μm. *B*, Close-up of an undefined flower. Arrow = stigmatic tissue. Bar = 150 μm. *C*, Joined stamen-like (*St?*) and pistillode-like (*Pd?*) structures. Bar = 300 μm. *D*, Adjoining stamens (*St*) and pistillode (*Pd*) near transition zone. Arrow = joined stamens. Bar = 300 μm. *E*, Pistillodes (*Pd*) among female flowers (*F*). Bar = 300 μm. *F*, Undefined floral structures (*A, B, C*) between stamens (*St*) and female flowers (*F*). Bar = 300 μm. *G*, Intermediate structure (arrow) between a typical cylindrical female flower (*F*) and a flattened pistillode (*Pd*). Bar = 300 μm.

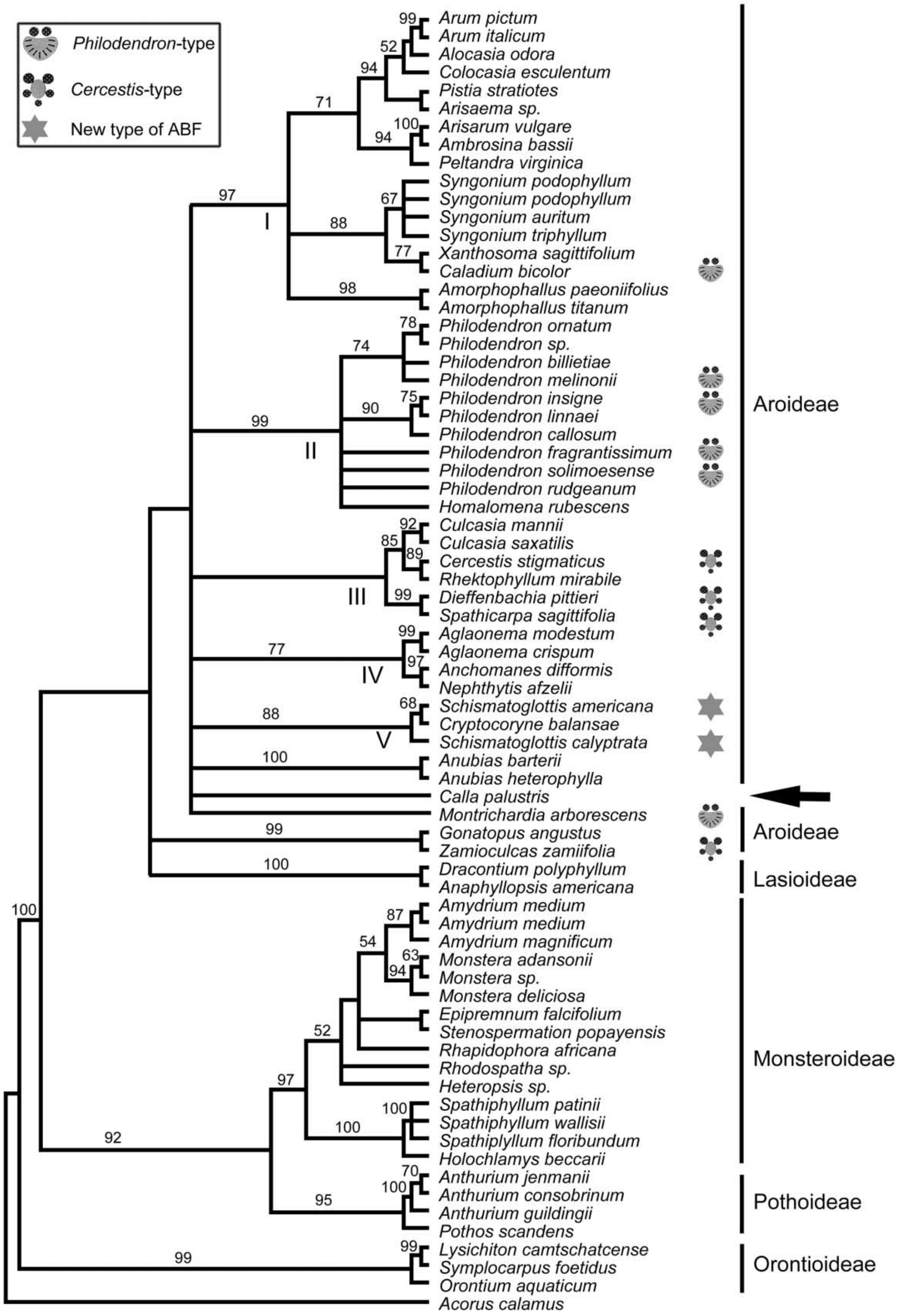

Fig. 8 Strict consensus of the 24 most parsimonious trees of 846 steps resulting from the phylogenetic analysis of 45 genera of Araceae on the basis of the *trn*L intron and *trn*L-F intergenic spacer. Bootstrap values higher than 50% are shown above branches. Subfamilial classification is based on Mayo et al. (1997). Diagrammatic representations of atypical bisexual flower (ABF) types are shown when known.

the morphological nature of atypical flowers in Aroideae in conjunction with phylogenetic analyses is warranted. Additional developmental data from other genera belonging to tribes related to the Schismatoglottideae will help clarify a possible correlation between phylogeny and development. Although this new cladistic analysis, based on the chloroplast *trn*L intron and *trn*L-F intergenic spacer, does not include all aroid genera, it corroborates in general, at the subfamily level, the molecular analysis of French et al. (1995) based on chloroplast DNA restriction site data, the analysis of Mayo et al. (1997) based on morphological and anatomical characters, and a previous study by Barabé et al. (2002*a*).

The unique morphology of the inflorescence of *Schismatoglottis* allowed us to complement the study of poorly known floral structures in the subfamily Aroideae. This study in combination with previous work shows that Araceae in general, and the subfamily Aroideae in particular, presents a great diversity of developmental features and a unique system to study the transition of different floral types within the same inflorescence.

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Literature Cited

Barabé D, C Bertrand 1996 Organogénie florale des genres *Culcasia* et *Cercestis* (Araceae). Can J Bot 74:898–908.

Barabé D, A Bruneau, F Forest, C Lacroix 2002*a* The correlation between development of atypical bisexual flowers and phylogeny in the Aroideae (Araceae). Plant Syst Evol 232:1–19.

Barabé D, S Forget 1988 Anatomie des fleurs fertiles et stériles de *Zamioculcas* (Araceae). Bull Mus Natl Hist Nat Sect B Adansonia Bot Phytochim 10:411–419.

Barabé D, C Lacroix 1999 Homeosis, morphogenetic gradient and the determination of floral identity in the inflorescences of *Philodendron solimoesense* (Araceae). Plant Syst Evol 219: 243–261.

——— 2000 Homeosis in Araceae flowers: the case of *Philodendron melinonii*. Ann Bot 86:479–491.

——— 2001 The developmental morphology of the flower of *Montrichardia arborescens* revisited. Bot J Linn Soc 135:413–420.

Barabé D, Lacroix C, B Jeune 2000 Development of the inflorescence and flower of *Philodendron fragrantissimum* (Araceae): a qualitative and quantitative study. Can J Bot 78:557–576.

——— 2002*b* Developmental morphology of normal and atypical flowers of *Philodendron insigne* (Araceae): a new case of homeosis. Can J Bot 80:1160–1172.

Barahona Carvajal ME 1977 Estudio morfológico comparativo de las inflorescencias de dos especies de Araceae: *Anthurium denudatum* Engler y *Philodendron radiatum* Schot. Rev Biol Trop 25: 301–333.

Berg RH 1994 A calcium oxalate-secreting tissue in branchlets of the Casuarinaceae. Protoplasma 183:29–36.

Borchert R 1984 Functional anatomy of the calcium-excreting system of *Gleditsia tricanthos* L. Bot Gaz 145:474–482.

Boubes C, D Barabé 1996 Développement de l'inflorescence et des fleurs du *Philodendron acutatum* (Araceae). Can J Bot 74:909–918.

——— 1997 Flower and inflorescence development in *Montrichardia arborescens* (L .) Schott (Araceae). Int J Plant Sci 158:408–417.

Buzgo M 1994 Inflorescence development of *Pistia stratiotes* (Araceae). Bot Jahrb Syst 115:557–570.

——— 2001 Flower structure and development of Araceae compared with Alismatids and Acoraceae. Bot J Linn Soc 136:393–425.

Cabrera LI, GA Salazar, MW Chase, SJ Mayo 2003 Phylogenetics of Araceae and Lemnaceae: evidence from multiple plastid DNA data sets. Abstract. Monocots 3 Conference, Rancho Santa Ana Botanic Garden, Santa Ana, California, March.

Carvell WN 1989 Floral anatomy of the Pothoideae and Monsteroideae. (Araceae). PhD diss. Miami University, Oxford, Ohio.

Cho Y, JD Palmer 1999 Multiple acquisition via horizontal transfer of a group I intron in the mitochondrial *cox1* gene during evolution of the Araceae family. Mol Biol Evol 16:1155–1165.

D'Arcy WG, RC Keating, SL Buchmann 1996 The calcium oxalate package or so-called resorption tissue in some angiosperm anthers. Pages 159–190 *in* WG D'Arcy, RC Keating, eds. The anther: form, function and phylogeny. Cambridge University Press, Cambridge.

Duvall MR, MT Clegg, MW Chase, WD Clark, WJ Kress, HG Hills, LE Eguiarte, et al 1993 Phylogenetic hypotheses for the monocotyledons constructed from *rbcL* sequences. Ann Mo Bot Gard 80:607–619.

Eckardt T 1937 Untersuchungen über Morphologie, Entwicklungsgeschichte und systematische Bedeutung des pseudomonomeren Gynäceums. Nova Acta Leopold 5:3–112.

Engler A, K Krause 1912 Araceae-Philodendroideae-Philodendreae. Pages 1–134 *in* A Engler, ed. Das Pflanzenreich. Regni vegetabilis conspectus. IV. 23Da. Heft 55. Engelmann, Weinheim. Reprinted 1966 (Cramer).

Eyde RH, DH Nicolson, P Sherwin 1967 A survey of floral anatomy in Araceae. Am J Bot 54:478–497.

Fink S 1991*a* Comparative microscopical studies on the patterns of calcium oxalate distribution in the needles of various conifer species. Bot Acta 104:306–315.

——— 1991*b* The morphological distribution of bound calcium in needles of Norway spruce (*Picea abies* [L.] Karst.). New Phytol 119: 33–40.

Franceschi VR, HT Horner 1980 Calcium oxalate crystals in plants. Bot Rev 46:361–427.

French JC 1985*a* Patterns of endothecial wall thickenings in Araceae: subfamilies Calloideae, Lasioideae, and Philodendroideae. Bot Gaz 146:521–533.

——— 1985*b* Patterns of endothecial wall thickenings in Araceae: subfamilies Pothoideae and Monsteroideae. Am J Bot 72:472–486.

——— 1986*a* Ovular vasculature of Araceae. Bot Gaz 147:478–495.

——— 1986*b* Patterns of stamen vasculature in the Araceae. Am J Bot 73:434–449.

French JC, MG Chung, YK Hur 1995 Chloroplast DNA phylogeny of the Ariflorae. Pages 255–275 *in* PJ Rudall, PJ Cribb, DF Cutler, CJ Humphries, eds. Monocotyledons: systematics and evolution. Vol 1. Royal Botanic Gardens, Kew.

Grayum MH 1990 Evolution and phylogeny of the Araceae. Ann Mo Bot Gard 77:627–697.

Hay A, Yuzammi 2000 Schismatoglottidae (Araceae) in Malesia I-*Schismatoglottis*. Telopea 9:1–178.

Hotta M 1971 Study of the family Araceae: general remarks. Jap J Bot 20:269–310.

Kuo-Huang L 1992 Ultrastructural study on the development of crystal-forming sclereids in *Nymphaea tetragona*. Taiwania 37: 104–113.

Mayo SJ 1986 Systematics of *Philodendron* Schott (Araceae) with special reference to inflorescence characters. PhD thesis. University of Reading.

——— 1989 Observations of gynoecial structure in *Philodendron* (Araceae). Bot J Linn Soc 100:139–172.

Mayo SJ, J Bogner, PC Boyce 1997 The genera of Araceae. Royal Botanic Gardens, Kew.

Oladele FA 1982 Development of the crystalliferous cuticule of *Chamaecyparis lawsoniana* (A. Murr.) Parl. (Cupressaceae). Bot J Linn Soc 84:273–288.

Pennisi SV, DB McConnell, LB Gower, ME Kane, T Lucansky 2001 Periplasmic cuticular calcium oxalate crystal deposition in *Dracaena sanderiana*. New Phytol 1459:209–218.

Prychid C, PJ Rudall 2000 Distribution of calcium oxalate crystals in Monocotyledones. Pages 159–162 *in* KL Wilson, DA Morrison, eds. Monocots: systematics and evolution. CSIRO, Melbourne.

Soltis DE, PS Soltis, MW Chase, ME Mort, DC Albach, M Zanis, V Savolainen, et al 2000 Angiosperm phylogeny inferred from 18S rDNA, *rbcL*, and *atpB* sequences. Bot J Linn Soc 133:381–461.

Swofford DL 2000 PAUP*: phylogenetic analysis using parsimony (and other methods), version 4. Sinauer, Sunderland, Mass.

Uhlarz H 1982 Typologische und ontogenetische untersuchungen an *Spathicarpa sagittifolia* Schott (Araceae): wuchsform und infloreszenz. Beitr Biol Pflanz 57:389–429.

——— 1986 Zum problem des "blattlosen Sprosses": morphologie und anatomie der infloreszenz von *Pinellia tripartita* (Blume) Schott (Araceae, Aroideae). Beitr Biol Pflanz 61:241–282.

Vladimirova SV 1996 Anatomical and morphological plasticity of the periclinal chimera *Dracaena sanderiana* "Ribbon" Hort. Sander ex M.T. Mast. (Agavaceae) in reponse to four light intensities. MS thesis. University of Florida, Gainesville.