

Aspects of floral morphology in *Ambrosina* and *Arisarum* (Araceae)

Denis Barabé, Christian Lacroix, and Marc Gibernau

Abstract: The floral morphology of *Ambrosina* and *Arisarum* is analysed from a developmental and phylogenetic point of view. In *Arisarum*, there are atypical organs displaying male and female characteristics. This developmental study shows that the male flowers of *Ambrosina* are di- or tri-androus. A close phylogenetic relationship between *Ambrosina* and *Arisarum* is supported by their morphology. Both genera have the same type of pollen (ellipsoid, inaperturate, striate-reticulate) and the mode of dehiscence (by a longitudinal slit) of the thecae. In *Arisarum*, the pollen is mixed with extracellular prismatic crystals of calcium oxalate.

Key words: atypical flowers, calcium oxalate crystals, flower development, phylogeny.

Résumé : La morphologie florale chez l'*Ambrosina* et l'*Arisarum* a été analysée d'un point de vue développemental et phylogénétique. Chez l'*Arisarum*, il existe des organes floraux atypiques présentant des caractéristiques mâle et femelle. Cette étude développementale démontre que les fleurs mâle de l'*Ambrosina* sont di- ou tri-andriques. La comparaison morphologique soutient une relation phylogénétique proche de l'*Ambrosina* et de l'*Arisarum*. Les deux genres ont en commun le même type de pollen (ellipsoïde et inaperturé) ainsi que le mode de déhiscence (fente longitudinale) par les thecae. Dans le genre *Arisarum*, le pollen est mélangé avec des cristaux extracellulaires d'oxalate de calcium.

Mots clés : fleurs atypiques, cristaux d'oxalate de calcium, développement floral, phylogénie.

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. Several species with unisexual flowers representing a number of genera have been investigated from the perspective of floral anatomy and developmental morphology (e.g., Engler and Krause 1912; Eckardt 1937; Eyde et al. 1967; Hotta 1971; Barahona Carvajal 1977; Uhlarz 1982, 1986; French 1985, 1986; Mayo 1986, 1989; Barabé and Forget 1988; Carvell 1989; Buzgó 1994, 2001). Recently, Barabé and collaborators (e.g., Barabé and Bertrand 1996; Barabé and Lacroix 1999; Barabé et al. 2000, 2002a) showed that the flowers of some genera in the Araceae have developmental features that can

be analysed from an ontogenetic and evolutionary perspective (Barabé et al. 2002b). Although floral development in genera belonging to the tribes Philodendreae and Culcasiae is well documented (Barabé and Bertrand 1996; Boubes and Barabé 1996; Barabé and Lacroix 1999; Barabé et al. 2000), there are few developmental studies of genera where the number of flowers per inflorescence is considerably reduced, such as in tribes Arisareae and Pistieae (Killian 1929, 1933; Buscalioni and Lanza 1937; Benzing 1969; Buzgó 1994). The tribes Arisareae and Ambrosineae consist of only one genus each, respectively: *Arisarum* with three species and *Ambrosina* with one species (Mayo et al. 1997).

This study complements the anatomical and morphological studies of *Arisarum* and *Ambrosina* already published by Killian (1929, 1933), Buscalioni and Lanza (1937), and Benzing (1969). More specifically, the floral morphology of these genera is analysed from a developmental and phylogenetic point of view. A molecular phylogenetic analysis of 46 genera of Araceae based on the chloroplast *trnL* intron and *trnL-F* intergenic spacer sequences that were recently produced by Barabé et al. (2004), and a cladogram developed by Mayo et al. (1997) based on anatomical and morphological data, will be used to discuss the phylogenetic position of *Arisarum* and *Ambrosina* in relation to flower developmental morphology. Our general goal is to assess whether the different floral types appearing on the inflorescences of members of the tribe Arisareae can be integrated into the phylogenetic pattern of the different types of unisex-

Received 15 May 2003. Published on the NRC Research Press Web site at <http://canjbot.nrc.ca> on 15 March 2004.

D. Barabé.¹ Institut de recherche en biologie végétale, Jardin botanique de Montréal, 4101 Sherbrooke Est, Montréal, QC H1X 2B2, Canada.

C. Lacroix. Department of Biology, University of Prince Edward Island, 550 University Avenue, Charlottetown, PE C1A 4P3, Canada.

M. Gibernau. Laboratoire d'Evolution & Diversité Biologique, Université de Toulouse III, 118 Route de Narbonne, Bât. 4R3-B2, 31062 Toulouse CEDEX 4, France.

¹Corresponding author (e-mail: denis.barabe@umontreal.ca).

ual flowers previously recognized in the subfamily Aroideae (Barabé et al. 2002b).

Developmental studies often reveal particular features that are not visible on fully developed organs. This was the case, for example, with the accumulation of extracellular calcium oxalate crystals on floral organs in *Philodendron* (Barabé and Lacroix 2001; Barabé et al. 2002b), *Schismatoglottis*, and *Arum* (Barabé et al. 2003). We also attempt to confirm the presence of extracellular calcium oxalate crystals in flowers of *Arisarum*. The mode of release of oxalate crystals in this taxon will be compared with that of other genera exhibiting the same phenomenon.

The goals of this study are therefore (1) to further document poorly known developmental features in the tribe Arisareae such as the release of calcium oxalate crystals by floral organs in the subfamily Aroideae and (2) to compare the development of flowers of *Arisarum* and *Ambrosina* to other genera to further characterize the range of floral morphologies in the subfamily Aroideae.

Material and methods

Specimens of *Arisarum vulgare* Targioni-Tozzetti and *Ambrosina bassii* L. were collected in Corsica (October 2001 and 2002). Voucher specimens were deposited at the Herbarium Marie-Victorin (Mont.): *Barabé 178* (*A. vulgare*) and *Barabé 180* (*A. bassii*).

Twenty-two inflorescences of *Arisarum* and 17 inflorescences of *Ambrosina* at various stages of development were fixed in formalin – acetic acid – alcohol (1:1:9 by volume) for at least 24 h, and later transferred and stored in 70% ethanol. Inflorescences were dissected under a stereo microscope to expose the spadix and then dehydrated in a graded ethanol series to absolute ethanol. Dissected inflorescences were then dried in a LADD model 28000 critical point drier (LADD Research Industries, Williston, Vt.) using CO₂ as a transitional fluid, mounted on metal stubs, and ground with conductive silver paint. Specimens were sputter coated to approximately 30 nm with gold–palladium using a Denton Vacuum Desk II sputter coater (Moorestown, N.J.), and viewed with a Cambridge S604 scanning electron microscope (Cambridge, U.K.) with digital imaging capabilities (SEMICAPS®).

Results

In *Ambrosina*, the male and female zones are located on opposite faces of the spadix (Fig. 1A). The female zone consists of one gynoeceium located on the ventral face of the spadix (Fig. 1A). The male zone, located on the dorsal side of the spadix, consists of 16–24 thecae arranged more or less in two longitudinal rows of 8–11 thecae each (Fig. 1B). The thecae are oriented transversely and open by longitudinal slits. In each longitudinal row, the thecae are arranged in pairs or in groups of three (Fig. 1B, asterisks). The dorsal surface of the spadix is covered by glandular hair-like structures (Fig. 1C). At the base of the thecae, globular masses of cells that look like glandular structures can also be observed (Figs. 2A and 2B). The ovary is topped by a long style that curves toward the axis of the spadix (Fig. 1A). At anthesis, the discoid stigma is closely appressed to the surface of the

spadix, and the inaperturate pollen is extruded in irregular masses. Ellipsoid pollen grains can be observed among the glandular hairs on the dorsal surface of the spathe (Fig. 2C). The exine is striate–reticulate on nearly its entire surface, and verruculose at the extremities of the pollen grain (Fig. 2D).

In *Arisarum*, the female zone consists of 2–5 flowers located at the base of the spadix. The ovary is depressed to globose in shape. The narrow style is topped by a sub-hemispheric stigma consisting of elongated papillae (Figs. 3C and 3D). Extracellular calcium oxalate crystals are found on the stigmatic surface when the stigma is nearly mature (Fig. 4E).

The male flowers are monandrous (Fig. 3A). The anthers are circular and peltate. The thecae are apically confluent and dehisce along a single continuous slit (Figs. 3A and 4C). The pollen is ellipsoid–elongate and inaperturate, and mixed with extracellular prismatic crystals (Fig. 3B).

Above the male zone, there is a sterile appendix terminating in a massive apical knob with a smooth epidermal surface (Figs. 4A and 4B). In the intermediate zone between the female and male zones, there are atypical flowers with both staminal and pistillate characters. For example, in Fig. 4D, the atypical flower is characterized by a discontinuous stigmatic surface (arrow) and staminal portion (asterisk).

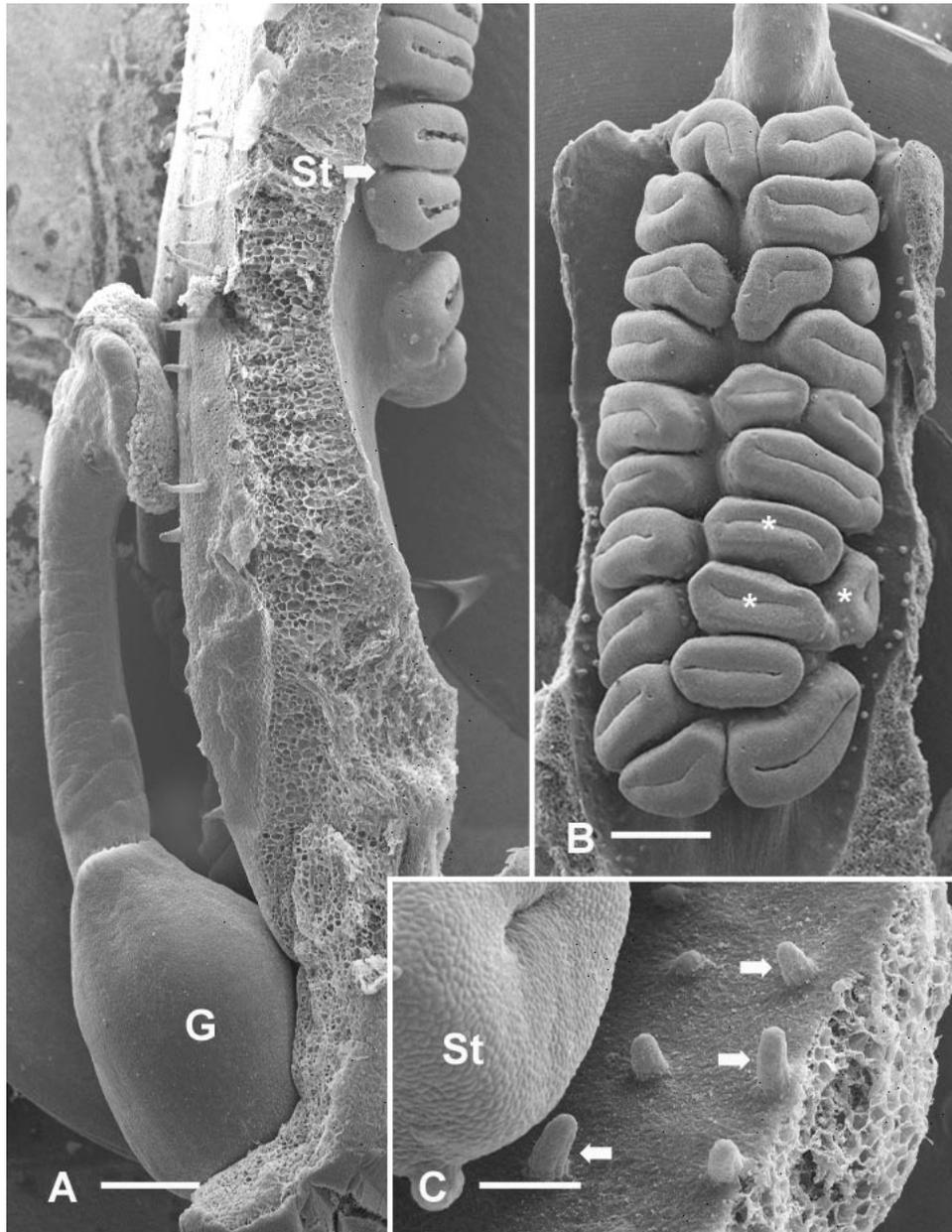
Discussion

Atypical organs in *Arisarum*

In *Arisarum* we observed a phenomenon that has previously been reported in a different genus, *Philodendron megalophyllum* (Barabé and Lacroix 2001): the presence of atypical organs displaying male and female characteristics (Fig. 4D). These intermediate organs, which represent teratological structures, have been reported in other angiosperm taxa (Guédès 1979). The intermediate nature of these organs indicates that they are under the physiological influence of both the neighbouring female and male flowers. Although the total number of organs on the inflorescence of *Arisarum* is much smaller compared with that of *Philodendron*, the presence of atypical bisexual structures was observed in both genera. This seems to indicate that the formation of atypical structures between the female and male zones represents a general tendency in the subfamily Aroideae.

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

Fig. 1. *Ambrosina bassii*. (A) Side view of a portion of the spadix showing the long-styled gynoecium (G) and the stamens (St). Scale bar = 750 μm . (B) Front view of entire group of stamens on the inflorescence. Asterisks represent a group of 3 thecae. Scale bar = 750 μm . (C) Surface of spadix facing the stamens (St) covered with glandular hairs (arrows). Scale bar = 150 μm .



by a few (1–5) vestigial stamens (Barabé and Bertrand 1996).

In *Arisarum*, atypical structures with a morphology intermediate between a stamen and an ovary are not homologous with ABFs observed in other genera. In contrast with *Cercestis* and *Philodendron*, ABFs with rudimentary or fully developed organs of both sexes were not observed. The atypical structures that are present in the intermediate zone between the female and male zones do not correspond to any type of ABFs that have been previously documented (Barabé et al. 2002b).

Stamens in *Ambrosina*

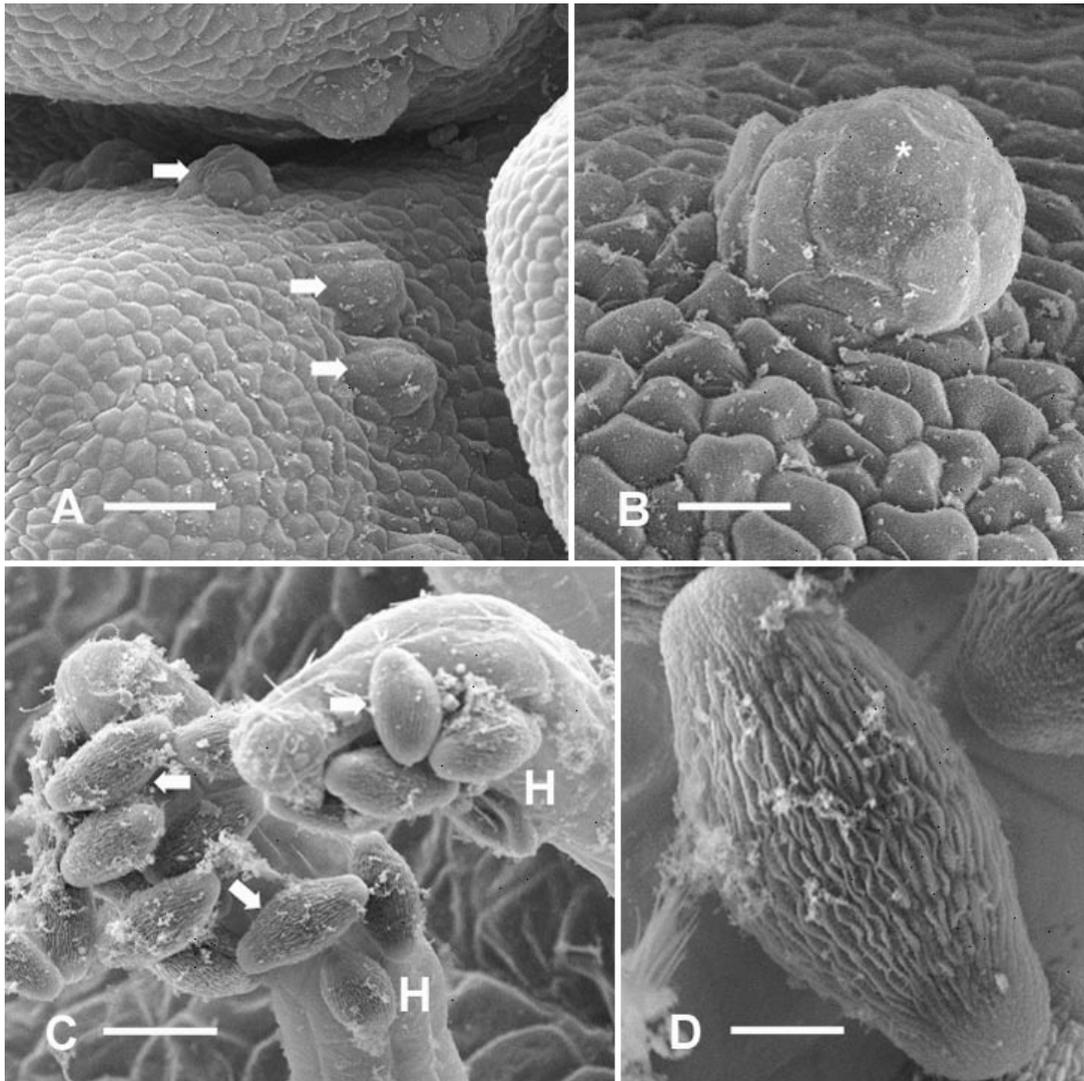
As noted by Mayo et al. (1997), the morphological inter-

pretation of the male flower remains problematic. They did not agree completely with the interpretation of Engler (1920a) and Benzing (1969), who state that the male flower is diandrous. Our results show that thecae are generally found in pairs (Fig. 1A) or in groups of three (Fig. 1B), supporting the interpretation of Benzing (1969). On the inflorescence represented in Fig. 1B, for example, there is a total of 23 thecae, corresponding to 7 diandrous flowers and 3 triandrous flowers (asterisks).

Phylogeny and morphology

A recent molecular phylogenetic analysis (Barabé et al. 2004) places *Arisarum* as the sister group of *Ambrosina*. The *Arisarum*–*Ambrosina* cluster forms a monophyletic group

Fig. 2. *Ambrosina bassii*. (A) Surface view of stamen showing glandular-like outgrowths (arrows). Scale bar = 75 μm . (B) Higher magnification of an outgrowth (*) referred to in A. Scale bar = 30 μm . (C) Glandular hairs (H) of the spathe covered with pollen grains (arrows). Scale bar = 30 μm . (D) Higher magnification of pollen grain. Scale bar = 7.5 μm .



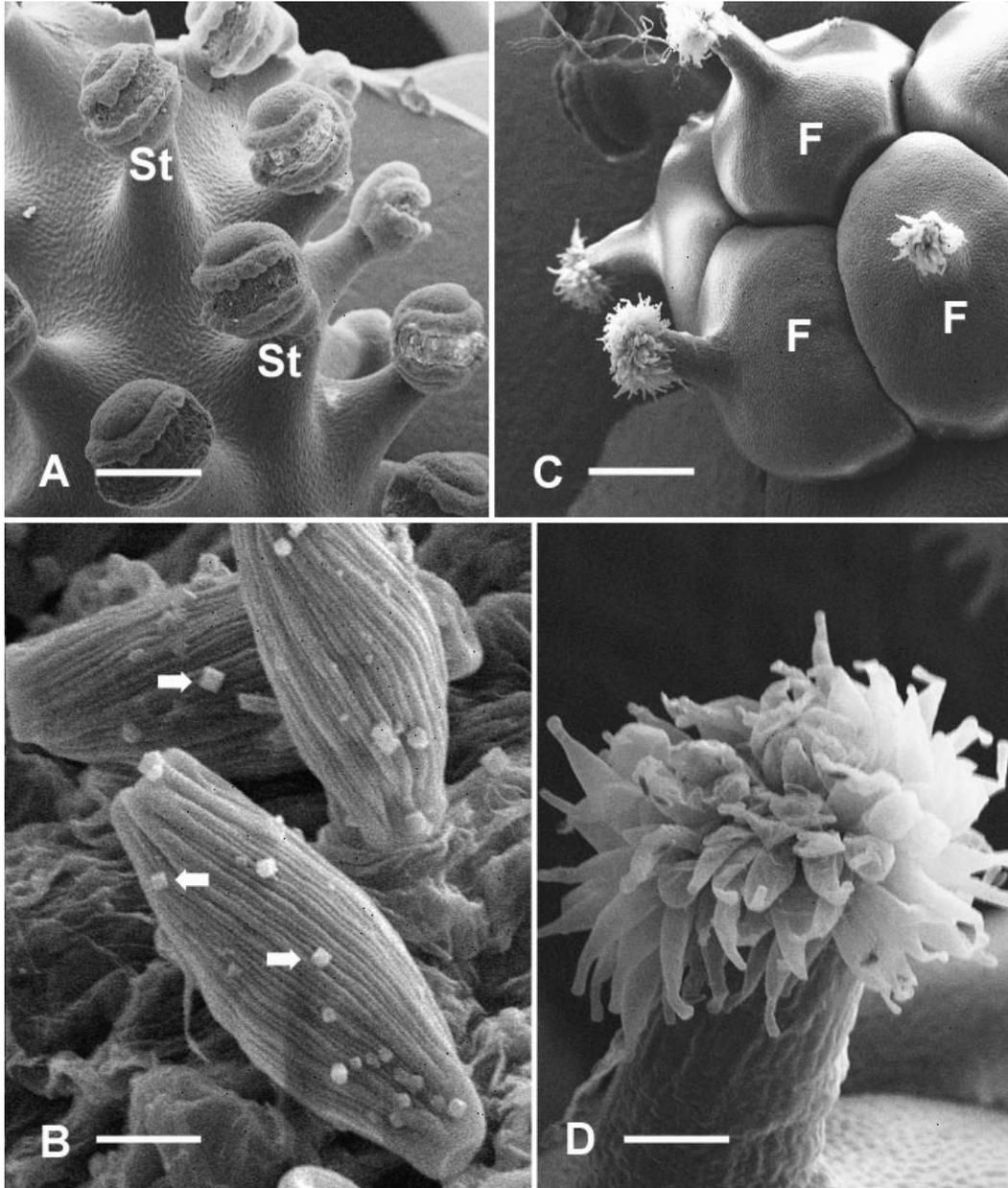
with the genus *Peltandra*. This result is in accordance with results published by French et al. (1995). The genus *Pistia* appears in another clade as the sister group of the genus *Arisaema*. This clade also includes the genera *Arum*, *Alocasia*, and *Colocasia*. In the cladogram of Mayo et al. (1997), *Ambrosina* is placed in the same cluster as *Pistia*, with *Arisarum* as sister group. The close molecular phylogenetic relationship between *Arisarum* and *Ambrosina* is supported at the morphological level by the type of pollen (ellipsoid, inaperturate, striate-reticulate) and the mode of dehiscence of the thecae (by a longitudinal slit). However, *Pistia* also has striate, inaperturate ellipsoid pollen like *Ambrosina* and *Arisarum*. The overall morphology of the spadix of *Ambrosina* is also similar to that of *Pistia* (Buscalioni and Lanza 1937). Moreover, the inflorescence of *Pistia* shares common morphological features with the group Cryptocoryninae (Engler 1920b; Buzgo 1994).

Calcium oxalate crystals

Extracellular crystal deposition on the epidermal surface

is a characteristic feature of many lichens (Garty et al. 2002) and gymnospermous species (Oladale 1982; Fink 1991a). In angiosperms, this phenomenon was reported for Casuarinaceae (Berg 1994), *Dracaena* (Fink 1991b; Pennisi et al. 2001), *Gleditsia* (Borchett 1984), *Nymphaea* (Franceschi and Horner 1980; Kuo-Huang 1992), *Sempervivum* (Fink 1991b; Vladimirova 1996), and *Stelis* (Chase and Peacor 1987). However, in a recent survey (Prychid and Rudall 1999, 2000) of the distribution of calcium oxalate crystals in monocotyledons, there is no mention of extracellular crystals, although this phenomenon had been reported in *Dracaena* (Fink 1991b), *Nymphaea* (Franceschi and Horner 1980), and *Stelis* (Chase and Peacor 1987). This seems to indicate that the presence of extracellular crystals exudates is uncommon in monocotyledons. 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 *Zantedeschia*. Recent developmental studies have shown that extracellular calcium oxalate crystals are visible on the surface of the api-

Fig. 3. *Arisarum vulgare*. (A) Mature stamens (St) at dehiscence. Scale bar = 750 μm . (B) Pollen grains covered with calcium oxalate crystals (arrows). Scale bar = 7.5 μm . (C) Fully mature female flowers (F). Scale bar = 750 μm . (D) Higher magnification of stigma showing stigmatic papillae. Scale bar = 150 μm .

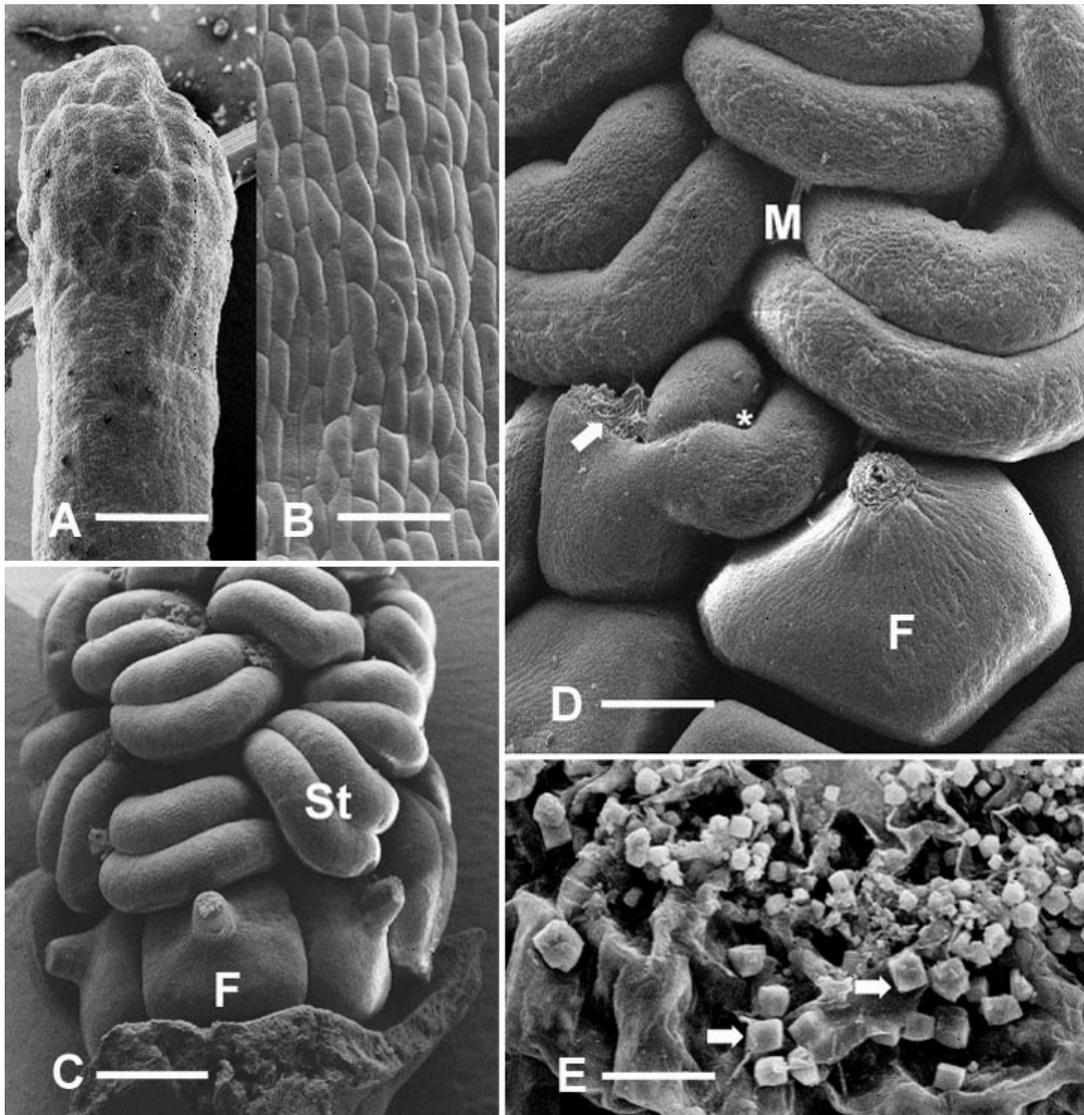


cal portion of nearly mature stamens of many species of *Philodendron*. These exudates form a subglobular mass on the surface of the epidermis (Barabé and Lacroix 2001; Barabé et al. 2002b). In *Philodendron*, the oxalate packages were not observed on the mature stamens after the opening of the spathe. However, in some species (e.g., *P. megalophyllum*) prismatic crystals and raphides are mixed with pollen at dehiscence (data not included). This indicates that oxalate crystals produced during early stages of development remain enclosed in the spathe until dehiscence. In *Schismatoglottis calyptrata*, as in *Arisarum*, the accumulation of extracellular calcium oxalate crystals occurs when the stamens are mature and the stigmatic surface is receptive

(Barabé et al. 2004). In Araceae, as with other plant species, extracellular oxalate crystals could play a biotic role in inhibiting herbivory (Franceschi and Horner 1980) or enhancing pollination (Chase and Peacor 1987; D'Arcy et al. 1996). Extracellular crystals could also be related to pollination by providing a visual signal or a scent that attracts insects (Chase and Peacor 1987; D'Arcy et al. 1996).

By using the method of D'Arcy et al. (1996) to take up pollen and associated crystals, we observed that the pollen of *Arisarum* is mixed with raphides at the time of dehiscence. However, there were no prismatic crystals mixed with the raphides on the slides we observed. This is probably due to the great variation that may occur in the quantity

Fig. 4. *Arisarum vulgare*. (A) Tip of spadix showing verrucose surface. Scale bar = 750 μm . (B) Smooth epidermal surface of spadix. Scale bar = 75 μm . (C) Nearly mature basal portion of spadix showing female flowers (F) and stamens (St). Scale bar = 750 μm . (D) Area of spadix between the female and male zones showing aberrant flower with stigmatic portion (arrow) and staminate portion (*). Scale bar = 300 μm . (E) Calcium oxalate crystals (arrows) on nearly mature stigma. Scale bar = 15 μm .



of crystals liberated by an inflorescence. For example, the presence of raphides mixed with pollen range from nonexistent to abundant in *Arisarum* (data not included).

Free crystals were observed on the stigmatic surface in *Arisarum*, as in *Philodendron melinonii* (Barabé and Lacroix 2000) and *P. insigne* (Barabé et al. 2002b). As for the presence of oxalate crystals on stigmatic surfaces, Miaja et al. (1998–1999) reported the presence of exudates of calcium oxalate crystals on the stigmatic surface of *Vitis vinifera* L. 'Barbera'. However, they did not discuss the possible implications of this observation. It is possible that the presence of oxalate crystals on the stigma could improve the success of pollen germination (Stephenson et al. 1992). For many species, boron and calcium are also required for pollen tube growth (Richards 1986; White and Broadley 2003). Calcium, found on the surface of some pollen grains, is often required for germination and has been implicated in the successful germination of large numbers of pollen grains in in-

stances where only a few pollen grains cannot germinate. Calcium is also involved in pectin synthesis and control of osmotic conditions (Richards 1986).

The unique morphology of the inflorescences of *Arisarum* and *Ambrosina* 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, have a great diversity of developmental features related to floral biology and phylogeny. In that context, developmental studies remain essential to interpret overall morphology from a phylogenetic perspective.

Acknowledgments

We are grateful to Paul and Jacky Quilichini for their great hospitality in Eccica during our stay in Corsica. This research was supported in part by grants from the Natural

Sciences and Engineering Research Council of Canada (NSERC) to D.B. (41794-98) and C.L. (121550-01).

References

- Barabé, D., and Bertrand, C. 1996. Organogénie florale des genres *Culcasia* et *Cercestis* (Araceae). *Can. J. Bot.* **74**: 898–908.
- Barabé, D., and Forget, S. 1988. Anatomie des fleurs fertiles et stériles de *Zamioculcas* (Araceae). *Bull. Mus. Nat. Hist. Nat. Sect. B Adansonia Bot. Phytochim.* **10**: 411–419.
- Barabé, D., and Lacroix, C. 1999. Homeosis, morphogenetic gradient and the determination of floral identity in the inflorescences of *Philodendron solimoense* (Araceae). *Plant Syst. Evol.* **219**: 243–261.
- Barabé, D., and Lacroix, C. 2000. Homeosis in the flower of the Araceae: the case of *Philodendron melinonii* (Araceae). *Ann. Bot. (Lond.)*, **86**: 479–491.
- Barabé, D., and Lacroix, C. 2001. The developmental floral morphology of *Montrichardia arborescens* (Araceae) revisited. *Bot. J. Linn. Soc.* **135**: 413–420.
- Barabé, D., Lacroix, C., and Jeune, B. 2000. Development of the inflorescence and flower of *Philodendron fragrantissimum* (Araceae): a qualitative and quantitative study. *Can. J. Bot.* **78**: 557–576.
- Barabé, D., Lacroix, C., and Jeune, B. 2002a. Developmental morphology of normal and atypical flowers of *Philodendron insigne* (Araceae): a new case of homeosis. *Can. J. Bot.* **80**: 1160–1172.
- Barabé, D., Bruneau, A., Forest, F., and Lacroix, C. 2002b. The correlation between development of atypical bisexual flowers and phylogeny in the Aroideae (Araceae). *Plant Syst. Evol.* **232**: 1–19.
- Barabé, D., Lacroix, C., and Gibernau, M. 2003. Development of the flower and inflorescence of *Arum italicum* (Araceae). *Can. J. Bot.* **81**: 622–632.
- Barabé, D., Lacroix, C., Bruneau, A., Archambault, A., and Gibernau, M. 2004. Floral development and phylogenetic position of *Schismatoglottis* (Araceae). *Int. J. Plant. Sci.* **165**. In press.
- Barahona Carvajal, M.E. 1977. Estudio morfológico comparativo de las inflorescencias de dos especies de Araceae: *Anthurium denudatum* Engler y *Philodendron radiatum* Schott. *Rev. Biol. Trop.* **25**: 301–333. [In Spanish.]
- Benzing, L. 1969. Beitrag zur Klärung der Verwandtschaftsverhältnisse der Tribus Aroideae-Araceae) auf vergleichend-blütenmorphologischer Grundlage. Mainz. Ph.D. thesis, University Mainz, Germany. [In German.]
- Berg, R.H. 1994. A calcium oxalate-secreting tissue in branchlets of the Casuarinaceae. *Protoplasma*, **183**: 29–36.
- Borchet, R. 1984. Functional anatomy of the calcium-excreting system of *Gleditsia tricanthos* L. *Bot. Gaz.* **145**: 474–482.
- Boubes, C., and Barabé, D. 1996. Développement des inflorescences et des fleurs du *Philodendron acutatum* (Araceae). *Can. J. Bot.* **74**: 909–918.
- Buscalioni, L., and Lanza, D. 1937. La basi morfologiche, anatomiche e teratologiche della nuova famiglia delle Pistaceae (Buscalioni e Lanza) rappresentata dei due generi *Pistia* ed *Ambrosinia*. *Malpighia*, **34**: 103–180. [In Italian.]
- Buzgó, M. 1994. Inflorescence development of *Pistia stratiotes* (Araceae). *Bot. Jahrb.* **115**: 557–570.
- Buzgó, M. 2001. Flower structure and development of Araceae compared with alismatids and Acoraceae. *Bot. J. Linn. Soc.* **136**: 393–425.
- Carvell, W.N. 1989. Floral anatomy of the *Pothoideae* and *Monsteroideae* (Araceae). Ph.D. thesis, Department of Botany, Miami University, Oxford, Ohio.
- Chase, M.W., and Peacor, D.R. 1987. Crystals of calcium oxalate hydrate on the perianth of *Stelis* SW. *Lindleyana*, **2**: 91–94.
- D'Arcy, W.G., Keating, R.C., and Buchmann, S.L. 1996. The calcium oxalate package or so-called resorption tissue in some angiosperm anthers. *In* The anther: form, function and phylogeny. Edited by W.G. D'Arcy and R.C. Keating. Cambridge University Press, Cambridge. pp. 159–190.
- Eckardt, T. 1937. Untersuchungen über Morphologie, Entwicklungsgeschichte und systematische Bedeutung des pseudomonomeren Gynoeceums. *Nova Acta Leopoldina*, **5**: 3–112. [In German.]
- Engler, A. 1920a. Araceae, Pars Generalis. *In* Das Pflanzenreich IV.23. Edited by A. Engler. Engelmann, Leipzig. pp. 1–71. [In German.]
- Engler, A. 1920b. Araceae-Aroideae, Araceae-Pistioideae. *In* Das Pflanzenreich. Regni vegetabilis conspectus. IV.23F. Edited by A. Engler. Engelmann, Leipzig. pp.1–274. [In German.]
- Engler, A., and Krause, K. 1912. Araceae-Philodendroideae-Philodendreae. *In* Das Pflanzenreich. Regni vegetabilis conspectus. IV. 23Da. Heft 55. Edited by A. Engler. Engelmann, Leipzig. pp.1–134. [In German.]
- Eyde, R.H., Nicolson, D.H., and Sherwin, P. 1967. A survey of floral anatomy in Araceae. *Am. J. Bot.* **54**: 478–479.
- Fink, S. 1991a. Comparative microscopical studies on the patterns of calcium oxalate distribution in the needles of various conifer species. *Bot. Acta*, **104**: 306–315.
- Fink, S. 1991b. The morphological distribution of bound calcium in needles of Norway spruce [*Picea abies* (L.) Karst.]. *New Phytol.* **119**: 33–40.
- Franceschi, V.R., and Horner, H.T. 1980. Calcium oxalate crystals in plants. *Bot. Rev.* **46**: 361–427.
- French, J.C. 1985. Patterns of endothelial wall thickenings in Araceae: subfamilies *Pothoideae* and *Monsteroideae*. *Am. J. Bot.* **72**: 472–486.
- French, J.C. 1986. Ovular vasculature of Araceae. *Bot. Gaz.* **147**: 478–495.
- French, J.C., Chung, M.G., and Hur, Y.K. 1995. Chloroplast DNA phylogeny of the Ariflorae. *In* Monocotyledons: systematics and evolution. Vol. I. Edited by P.J. Rudall, P.J. Cribb, D.F. Cutler, and C.J. Humphries. Royal Botanic Gardens, Kew. pp. 255–275.
- Garty, J., Kunin, P., Delarea, J., and Weiner, S. 2002. Calcium oxalate and sulphate-containing structures on the thallial surface of the lichen *Ramalia lacera*: response to polluted air and simulated acid rain. *Plant Cell Environ.* **25**: 1591–1604.
- Guédès, M. 1979. Morphology of seed-plants. *J. Cramer, Vaduz.*
- Hotta, M. 1971. Study of the family Araceae: general remarks. *Jpn. J. Bot.* **20**: 269–310.
- Killian, C. 1929. Développement et biologie de l'*Ambrosinia Bassii* L. 1^{ère} partie. *Bull. Soc. Hist. Nat. Afr. Nord*, **20**: 257–278.
- Killian, C. 1933. Développement, biologie et répartition de l'*Ambrosinia Bassii* L. 2^e partie. *Bull. Soc. Hist. Nat. Afr. Nord*, **24**: 259–294.
- Kuo-Huang, L. 1992. Ultrastructural study on the development of crystal-forming sclereids in *Nymphaea tetragona*. *Taiwania*, **37**: 104–113.
- Mayo, S.J. 1986. Systematics of *Philodendron* Schott (Araceae) with special reference to inflorescence characters. Ph.D. thesis, Department of Botany, University of Reading, U.K.
- Mayo, S.J. 1989. Observations of gynoeceal structure in *Philodendron* (Araceae). *Bot. J. Linn. Soc.* **100**: 139–172.

- Mayo, S.J., Bogner, J., and Boyce, P.C. 1997. The genera of Araceae. Royal Botanic Gardens, Kew.
- Miaja, M. L., Porporato, M. Caramiello, R., and Vallania, R. 1998–1999. Pollen–stigma interactions in *Vitis vinifera* L. cv. Barbera. *Allionia*, **36**: 35–40.
- Oladele, F.A. 1982. Development of the crystalliferous cuticle of *Chamaecyparis lawsoniana* (A. Murr.) Parl. (Cupressaceae). *Bot. J. Linn. Soc.* **84**: 273–288.
- Pennisi, S.V., McConnell, D.B., Gower, L.B., Kane, M.E., and Lucansky, T. 2001. Periplasmic cuticular calcium oxalate crystal deposition in *Dracaena sanderiana*. *New Phytol.* **149**: 209–218.
- Prychid, C., and Rudall, P.J. 1999. Calcium oxalate crystals in Monocotyledones: a review of their structure and systematics. *Ann. Bot. (Lond.)*, **84**: 725–739.
- Prychid, C., and Rudall, P.J. 2000. Distribution of calcium oxalate crystals in Monocotyledones. *In* *Monocots: systematics and evolution*. Edited by K.L. Wilson and D.A. Morrison. CSIRO, Melbourne. pp. 159–162.
- Richards, A.J. 1986. *Plant breeding systems*. George Allen and Unwin, London.
- Stephenson, A.G., Lau, T., Queseda, T., and Winsor, J.A. 1992. Factors that affect pollen performance. *In* *Ecology and evolution of plant reproduction*. Edited by R. Wyatt. Chapman and Hall, New York. pp. 119–136.
- Uhlarz, H. 1982. Typologische und ontogenetische Untersuchungen an *Spathicarpa sagittifolia* Schott (Araceae): Wuchsform und Infloreszenz. *Beitr. Biol. Pflanz.* **57**: 389–429. [In German.]
- Uhlarz, H. 1986. Zum Problem des “blattlosen Sprosses”: Morphologie und Anatomie der Infloreszenz von *Pinella tripartita* (Blume) Schott (Araceae, Aroideae). *Beitr. Biol. Pflanz.* **61**: 241–282. [In German.]
- Vladimirova, S.V. 1996. Anatomical and morphological plasticity of the periclinal chimera *D[raceana]. sanderiana* ‘Ribbon’ Hort. Sander ex M.T. Mast. (Agavaceae) in response to four light intensities. M.Sc. thesis, Horticultural Sciences, University of Florida, Fla., U.S.A.
- White, P.J., and Broadley, M.R. 2003. Calcium in plants. *Ann. Bot. (Lond.)*, **92**: 487–511.