SYSTEMATICS AND PHYLOGENY

Schismatoglottis and *Apoballis* (Araceae: Schismatoglottideae): A new example for the significance of pollen morphology in Araceae systematics

Silvia Ulrich,[1] Michael Hesse,[1] David Bröderbauer,[1] Sin Yeng Wong[2] & Peter C. Boyce[3]

1 *Department of Structural and Functional Botany, University of Vienna, 1030 Wien, Rennweg 14, Austria*
2 *Department of Plant Science and Environmental Ecology, Faculty of Resource Science and Technology, Universiti Malaysia Sarawak, 94300 Samarahan, Sarawak, Malaysia*
3 *Pusat Pengajian Sains Kajihayat [School of Biological Sciences], Universiti Sains Malaysia, 11800 USM, Pulau Pinang, Malaysia*
Author for correspondence: *Michael Hesse, michael.hesse@univie.ac.at*

Abstract Pollen characters in Araceae accord well with recent DNA-based phylogenies, and here we provide a new example of "compass needle" quality in Araceae on the basis of two closely related genera, *Schismatoglottis* and *Apoballis*. All investigated *Schismatoglottis* pollen is psilate (smooth pollen surface) with calcium crystals covering the pollen surface. By contrast, pollen of species transferred to recently resurrected *Apoballis* (*Apoballis acuminatissima* and *A. mutata*) is distinctively echinate (spiny). A unique layer covers the endexine of *Schismatoglottis*, and the whole pollen surface of *Apoballis*. Our findings strongly suggest that "*Schismatoglottis*" species with echinate pollen fall into the genus *Apoballis*. Moreover, all schismatoglottid taxa perform spathe movements during anthesis to control the movement of pollinators. The spathe movements of *Apoballis acuminatissima* clearly differ from those known in *Schismatoglottis* species, and indeed are so far unique for the entire family. This, together with differences in floral odour is strongly suggestive of differences in pollination ecology between the genera *Schismatoglottis* and *Apoballis*.

Keywords *Apoballis*; Araceae; pollen; *Schismatoglottis*; systematics; tropical Asia

■ INTRODUCTION

The genera of Araceae display a high morphological diversity, which extends to pollen wall morphology and exine sculpturing (Grayum, 1992; Mayo & al., 1997; Hesse, 2006). Tribe Schismatoglottideae is a well circumscribed basal clade within subfamily Aroideae (French & al., 1995; Hay, 1996; Mayo & al., 1997; Hay & Yuzammi, 2000; Keating, 2002, 2004; Cabrera & al., 2008; Cusimano & al., 2011). Schismatoglottideae is the most speciose and diverse aroid taxon in Borneo, with a very high percentage of endemic species (Wong & Boyce, 2010a). *Schismatoglottis* Zoll. & Moritzi is the largest genus of the tribe, with probably in excess of 250 species restricted to perhumid and everwet tropical Asia (Boyce & Wong, 2007). Recent taxonomic and systematic treatments for the genus include an alpha taxonomy (Hay & Yuzammi, 2000), and various additional novel taxa (e.g., Wong & Boyce, 2010a, b, c; Wong & al., 2010). One outcome of the partial phylogenetic treatment was the resurrection of the genus *Apoballis* Schott, and the transfer of 12 former *Schismatoglottis* species to *Apoballis* (Table 1). The genus *Apoballis* is well defined by morphological and molecular characters (Wong & Boyce, 2010a) and is sister to all other Schismatoglottideae.

The morphology of monocot pollen, especially of Araceae, has been studied iteratively since the pioneering work of Thanikaimoni (1969) and Zavada (1983). Pollen ornamentation of subfamily Aroideae (sensu Cabrera & al., 2008; Cusimano & al., 2011) is mostly psilate (smooth pollen surface) or echinate (spiny), but, disregarding *Calla* L., never reticulate. In contrast

to all other subfamilies the pollen wall in Aroideae (including Schismatoglottideae and excluding the puzzling case of *Calla*) lacks the common sporopollenin tectate-columellate exine. Instead, a non-sporopollenin, polysaccharidic outermost pollen wall layer (Weber & al., 1998, 1999), or polysaccharidic echini (Pacini & Juniper, 1983; Weber & al., 1998) cover the pollen wall (endexine). This polysaccharidic wall ornamentation is a unique feature of some Aroideae pollen, first documented in *Arum italicum* Mill. (Pacini & Juniper, 1983), and later in *Sauromatum venosum* (Ait.) Schott (Weber & al., 1998). It was also reported for *Pistia stratiotes* L., in which there are polysaccharidic plicae (ribs), and an additional thin polysaccharidic layer (Weber & al., 1999).

During our studies of the pollen ultrastructure of Araceae, the pollen of a *Schismatoglottis* species (at that time determined as *Schismatoglottis lancifolia* Hallier f. & Engl.) was revealed to be echinate. This, together with the occurrence of a thin outer acetolysis-resistant wall layer, was a novel finding for this tribe. Compared to all other investigated *Schismatoglottis* species and related genera with smooth pollen, this seemed to be, at first sight, a result of a possible taxon mix-up, for example with a spiny genus such as *Callopsis* Engl. (Weber, 2004). At that time no *Schismatoglottis* species was known to be spiny and the *Apoballis* resurrection was not yet published (Wong & Boyce, 2010a). *Schismatoglottis* pollen, as so far analysed, was reported to be psilate, typical for all Schismatoglottideae (Thanikaimoni, 1969; Grayum, 1992). A possible correlation between pollen ornamentation and pollinator type in Araceae was first postulated by Grayum (1986, 1992). Grayum (1986)

Table 1. The resurrected genus *Apoballis* and the 12 transferred *Schismatoglottis* species (Wong & Boyce, 2010a).

Species of the resurrected genus *Apoballis*	Basionym in *Schismatoglottis*
A. acuminatissima (Schott) S.Y. Wong & P.C. Boyce	*S. acuminatissima* Schott
A. belophylla (Alderw.) S.Y. Wong & P.C. Boyce	*S. belophylla* Alderw.
A. brevipes (Hook. f.) S.Y. Wong & P.C. Boyce	*S. brevipes* Hook. f.
A. grandiflora (Alderw.) S.Y. Wong & P.C. Boyce	*S. grandiflora* Alderw.
A. hastifolia (Hallier f. ex Engl.) S.Y. Wong & P.C. Boyce	*S. hastifolia* Hallier f. ex Engl.
A. javanica (Engl.) S.Y. Wong & P.C. Boyce	*S. javanica* Engl.
A. longicaulis (Ridl.) S.Y. Wong & P.C. Boyce	*S. longicaulis* Ridl.
A. mutata (Hook. f.) S.Y. Wong & P.C. Boyce	*S. mutata* Hook. f.
A. okadae (M. Hotta) S.Y. Wong & P.C. Boyce	*S. okadae* M. Hotta
A. ovata (Schott) S.Y. Wong & P.C. Boyce	*S. ovata* Schott
A. rupestris (Zoll. & Moritzi ex Zoll.) S.Y. Wong & P.C. Boyce	*S. rupestris* Zoll. & Moritzi ex Zoll.
A. sagittifolia (Alderw.) S.Y. Wong & P.C. Boyce	*S. sagittifolia* Alderw.

and Sannier & al. (2009) found a correlation between echinate pollen and fly pollination and psilate pollen with beetle pollination in Araceae. Regarding the differences in pollen ornamentation of *Schismatoglottis* and *Apoballis*, we studied movements of the inflorescence, which are indicative for pollination mode (Vogel, 1965), in order to check whether the differences in pollen ornamentation could be linked to differences in the pollinator type. Movements of the spathe are found throughout Araceae (Mayo & al., 1997), and are known to play an important role in controlling pollinator movements (Young, 1986; Ørgaard & Jacobsen, 1998; Vogel & Martens, 2000). In Schismatoglottideae all species so far observed display spathe movements (Boyce & Wong, 2007; Wong & Boyce, 2010b).

In this publication we present the first description of spathe movements in *Apoballis acuminatissima* (Schott) S.Y. Wong & P.C. Boyce, which are unique for the tribe and clearly differ from those observed in *Schismatoglottis*, and we use pollen as an additional character for generic delimitation of *Apoballis* and *Schismatoglottis*.

■ MATERIALS AND METHODS

Plant material. — Plant material was collected in Sarawak, Malaysian Borneo, the Munich Botanical Garden, and the Botanical Garden of the University of Vienna, studied fresh or stored in silica gel or in alcohol. The choice of species sampled in each genus was guided primarily by the availability of suitable material. A list of all voucher specimens is provided in the Appendix.

Preparation. — For light microscopy (LM), fresh and silica gel–dried material was rehydrated in water. Pollen was acetolysed for 5 minutes at 100°C (Erdtman, 1960; Hesse & Waha, 1989).

For scanning electron microscopy (SEM), pollen was rehydrated in water, dehydrated with 2,2-dimethoxypropane,

acetone and critical point–dried (Halbritter, 1998), and sputter coated with gold. Silica-dried pollen and pollen fixed in alcohol were only sputter coated with gold.

For transmission electron microscopy (TEM), anthers were rehydrated and fixed in 3% glutaraldehyde (GA), postfixed with 1% osmiumtetroxide (OsO_4) and 0.8% potassium hexacyanoferrate ($K_4Fe(CN)_6 \cdot 3H_2O$). Fixed material was dehydrated in 2,2-dimethoxypropane and then embedded in Agar's low viscosity resin (LV-Resin) and in Spurr's low-viscosity epoxy resin (Spurr, 1969; Agar Scientific, 2004). Sections (60–90 nm thick) were cut with a diamond knife on a Reichert Ultracut microtome. For common contrast, sections were stained with the modified Thiéry-test (Rowley & Dahl, 1977). All samples where stained with uranyl acetate followed by lead citrate (pictures not presented in this paper). The occurrence of polysaccharides was detected with the Thiéry-test (Thiéry, 1967). The detection of lipids followed the procedure of Rowley & Dahl (1977). For the detection of the endexine, sections were treated with 1% aqueous potassium permanganate solution ($KMnO_4$) (Hayat, 2000; Ulrich, 2006).

The course of anthesis in *Apoballis acuminatissima* was studied on several inflorescences of one plant in the greenhouses of the Botanical Garden of the University of Vienna. Movements of spathe and spadix were observed and documented in two inflorescences with a camera (Nikon Coolpix P 5000), which automatically took a picture every ten minutes. In addition, three further inflorescences were observed during daily visits.

■ RESULTS

Pollen analyses. — Pollen of *Apoballis* (Fig. 1; Table 2) and S*chismatoglottis* (Fig. 2; Table 2) is small and inaperturate (omniaperturate), but there are differences in pollen wall ultrastructure and sculpturing.

External morphology. — The most eye-catching difference between the pollen of the two genera is the external morphology. Pollen of all investigated species of *Apoballis* is echinate (spiny; Figs. 1, 3A–D) whereas the pollen of all investigated species of *Schismatoglottis* is psilate (smooth; Figs. 2, 3E–H). The echini (spines) of *Apoballis* consist of polysaccharids (Fig. 3D) and are resistant to acetolysis (Fig. 1G–J). Under the light microscope the pollen surface of *Schismatoglottis celebica* Engl. and *Schismatoglottis calyptrata* (Roxb.) Zoll. & Moritzi appears to be echinate (Fig. 2C, G). Scanning electron microscopy revealed that irregularly distributed calcium oxalate crystals of different size, not echini, cover the whole pollen surface (Fig. 2A–B, D–F). In contrast, the psilate pollen grains of *Schismatoglottis multiflora* Ridl. (Fig. 2H, K) are clumped together by large calcium crystals (Fig. 2I–J).

Internal structure. — The pollen wall of both genera consists of an intine (Fig. 3A–H; Table 2), a continuous, compact to spongy endexine (Fig. 3A–H; Table 2), and a thin layer
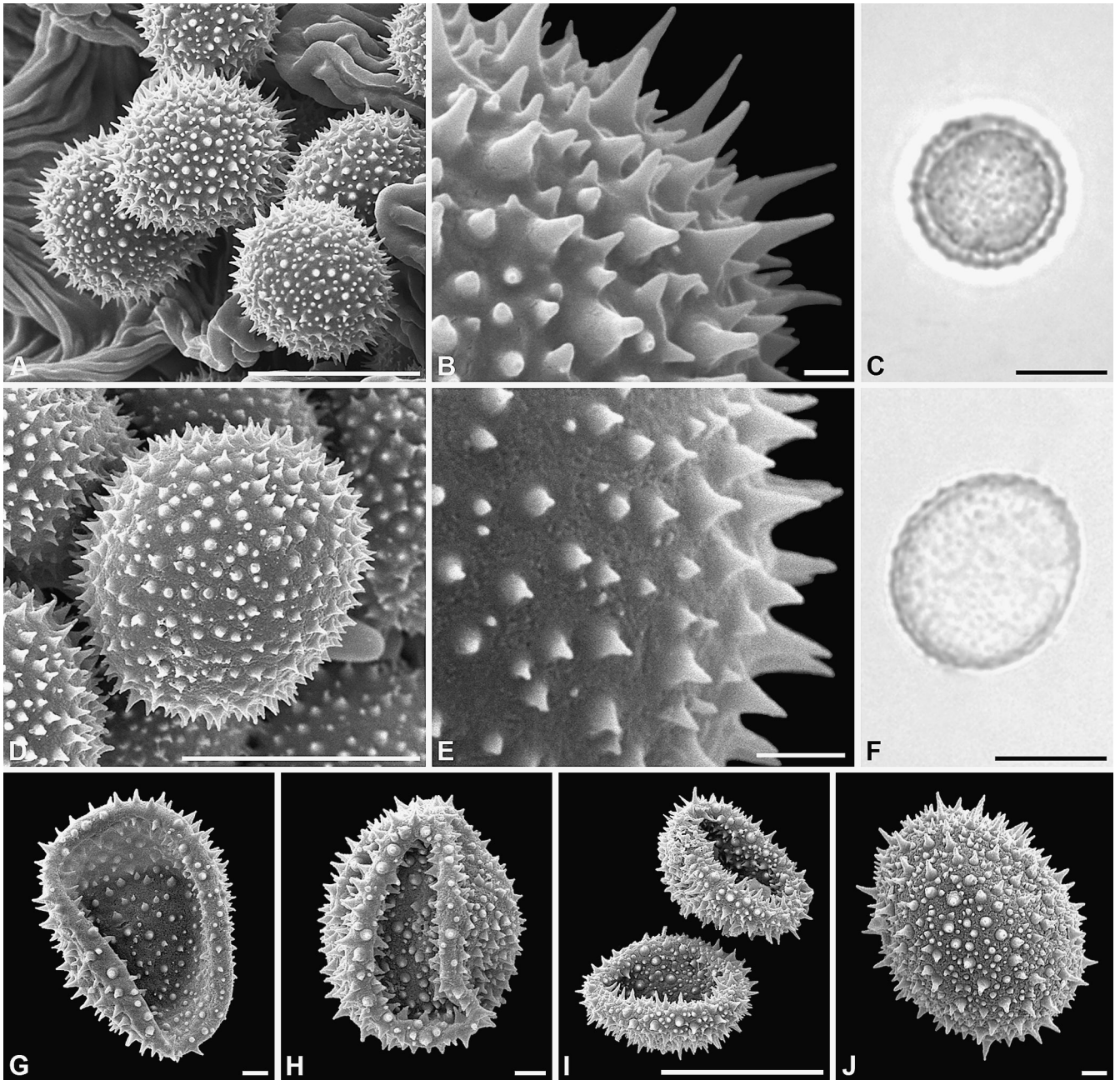
Fig. 1. Echinate pollen typical for *Apoballis*. **A–C,** *Apoballis acuminatissima*: **A,** pollen grains under SEM, air-dried; **B,** detail of pollen surface, air-dried; **C,** hydrated pollen grain in LM. **D–F,** *Apoballis mutata*: **D,** hydrated pollen grains under SEM, critical point–dried; **E,** detail of pollen surface; **F,** hydrated pollen grain under LM. **G–H,** acetolyzed pollen of *Apoballis mutata*; note that echini are acetolysis-resistant. **I–J,** acetolyzed pollen of *Apoballis acuminatissima*; note that echini are acetolysis-resistant. — Scale bars = 10 µm (A, C, D, F, G–J), 1 µm (B, E).

Table 2. Summary of the relevant pollen characters of all investigated species of Schismatoglottideae (n.i. = not investigated).

Genus / number of species	Species investigated	Size	Shape hydrated	Aperture	Ornamentation in LM-view
Apoballis Schott / 20	*A. acuminatissima* (Schott) S.Y. Wong & P.C. Boyce	Small	Spheroidal to elliptic	Inaperturate	Echinate
	A. mutata (Hook. f.) S.Y. Wong & P.C. Boyce	Small	Spheroidal to elliptic	Inaperturate	Echinate (Thanikaimoni, 1969)
	A. longicaulis (Ridl.) S.Y. Wong & P.C. Boyce	Small	n.i.	Inaperturate	Echinate (Thanikaimoni, 1969)
Bucephalandra Schott / 3	*B. motleyana* Schott	Small	Elliptic	Inaperturate	Psilate
Hestia S.Y. Wong & P.C. Boyce / 1	*H. longifolia* (Ridl) S.Y. Wong & P.C. Boyce	Small	Elliptic	Inaperturate	Psilate
Ooia S.Y. Wong & P.C. Boyce / 2	*O. grabowskii* (Engl.) S.Y. Wong & P.C. Boyce	Small	Elliptic	Inaperturate	Scabrate
Phymatarum M. Hotta / 1	*P. borneense* M. Hotta	Small	Elliptic	Inaperturate	Scabrate
Piptospatha N.E. Br. / 10	*P. viridistigma* P.C. Boyce, S.Y. Wong & Bogner	Small	Elliptic	Inaperturate	Scabrate
	P. ridleyi N.E. Br ex Hook. f.	Small	Elliptic	Inaperturate	Scabrate
Schismatoglottis Zoll. & Moritzi / 100	*S. calyptrata* (Roxb.) Zoll. & Moritzi	Small	Elliptic	Inaperturate	Scabrate
	S. celebica Engl.	Small	Elliptic	Inaperturate	Scabrate
	S. conoidea Engl.	Small	Elliptic	Inaperturate	Scabrate
	S. ifugaoensis S.Y. Wong, Bogner & P.C. Boyce	Small	Elliptic	Inaperturate	Scabrate
	S. matangensis S.Y. Wong	Small	Elliptic	Inaperturate	Scabrate
	S. modesta Schott	Small	Elliptic	Inaperturate	Scabrate
	S. motleyana (Schott) Engl.	Small	Elliptic	Inaperturate	Scabrate
	S. multiflora Ridl.	Small	Elliptic	Inaperturate	Scabrate
	S. roseospatha Bogner	Small	Elliptic	Inaperturate	Scabrate
	S. tecturata (Schott) Engl.	Small	Elliptic	Inaperturate	Scabrate
	S. viridissima A. Hay	Small	Elliptic	Inaperturate	Scabrate
Schottariella P.C. Boyce & S.Y. Wong / 1	*Schottariella mirifica* P.C. Boyce & S.Y. Wong	Small	Elliptic	Inaperturate	Scabrate

Cellular condition	Raphids	Crystals	Ornamentation in SEM-View	Intine	Endexine	Peculiarities	Illustrated
2 (& 3)	Raphids	Absent	Echinate	Bi-layered	Continuous, spongy	Thin outer layer, acetolysis resistant, polysaccharidic echini	Figs. 1, 3
2	Raphids	Absent	Echinate	Bi-layered	Continuous, spongy	Thin outer layer, acetolysis resistant, polysaccharidic echini	Fig. 1
n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	
2 (& 3)	Raphids	Absent	Verrucate	Bi-layered	Continuous, compact	Discontinuous outer ektexine (verrucate)	
2	Raphids	Small	Psilate, with crystals	n.i.	n.i.	n.i.	
3 (& 2)	Raphids	Absent	Psilate	Bi-layered	Continuous, compact	No outer ektexine layer	
2	Raphids	Absent	Psilate	Bi-layered			
3 (& 2)	Raphids	Absent	Psilate	n.i.	n.i.	n.i.	
n.i.	n.i.	Absent	n.i.	n.i.	n.i.	n.i.	
2	Raphids	Small	Psilate, with crystals	Bi-layered	Continuous, spongy	Thin outer layer, acetolysis-resistant	Fig. 2
2	Raphids	Small & large	Psilate, with crystals	Bi-layered	Continuous, spongy	Thin outer layer, acetolysis-resistant	Figs. 2, 3
2	Raphids	Small	Psilate, with crystals	n.i.	n.i.	n.i.	
2	Raphids	Small	Psilate	n.i.	n.i.	n.i.	
2 (& 3)	Raphids	Small	Psilate, with crystals	n.i.	n.i.	n.i.	
2 (&3)	Raphids	Small	n.i.	n.i.	n.i.	n.i.	
2	Raphids	Small & large	Psilate, with crystals	n.i.	n.i.	n.i.	
2 (& 3)	n.i.	Large	Psilate with crystals	Bi-layered	Continuous, spongy	Thin outer layer, acetolysis-resistant	Fig. 2
n.i.	n.i.	Absent	Psilate (Halbritter, unpub. data)	n.i.	n.i.	n.i.	
2 (& 3)	n.i.	Small	Psilate (Grayum, 1992)	n.i.	n.i.	n.i.	
2 (& 3)	Raphids	Small	Psilate with crystals	n.i.	n.i.	n.i.	
2 (& 3)	n.i.	Absent	Psilate	Bi-layered	Continuous, spongy	Thin outer layer (ektexine); holes between ektexine and endexine	

covering the whole pollen surface (Fig. 3A–H; Table 2). The intine always stains electron-lucent (Fig. 3A–C, E–G) except with the Thiéry-test (Fig. 3D, H). The compact to spongy endexine of the investigated species appeared electron-dense (Fig. 3A, C–H) or electron-lucent (Fig. 3B), depending on

the staining method. The outer pollen wall layer of *Apoballis acuminatissima* pollen was only clearly visible after the Lipid-test (Fig. 3C). In contrast to this, the outer pollen wall layer of *Schismatoglottis celebica* pollen stained differently, depending on the staining method. After the Thiéry-Test (Fig. 3H), the
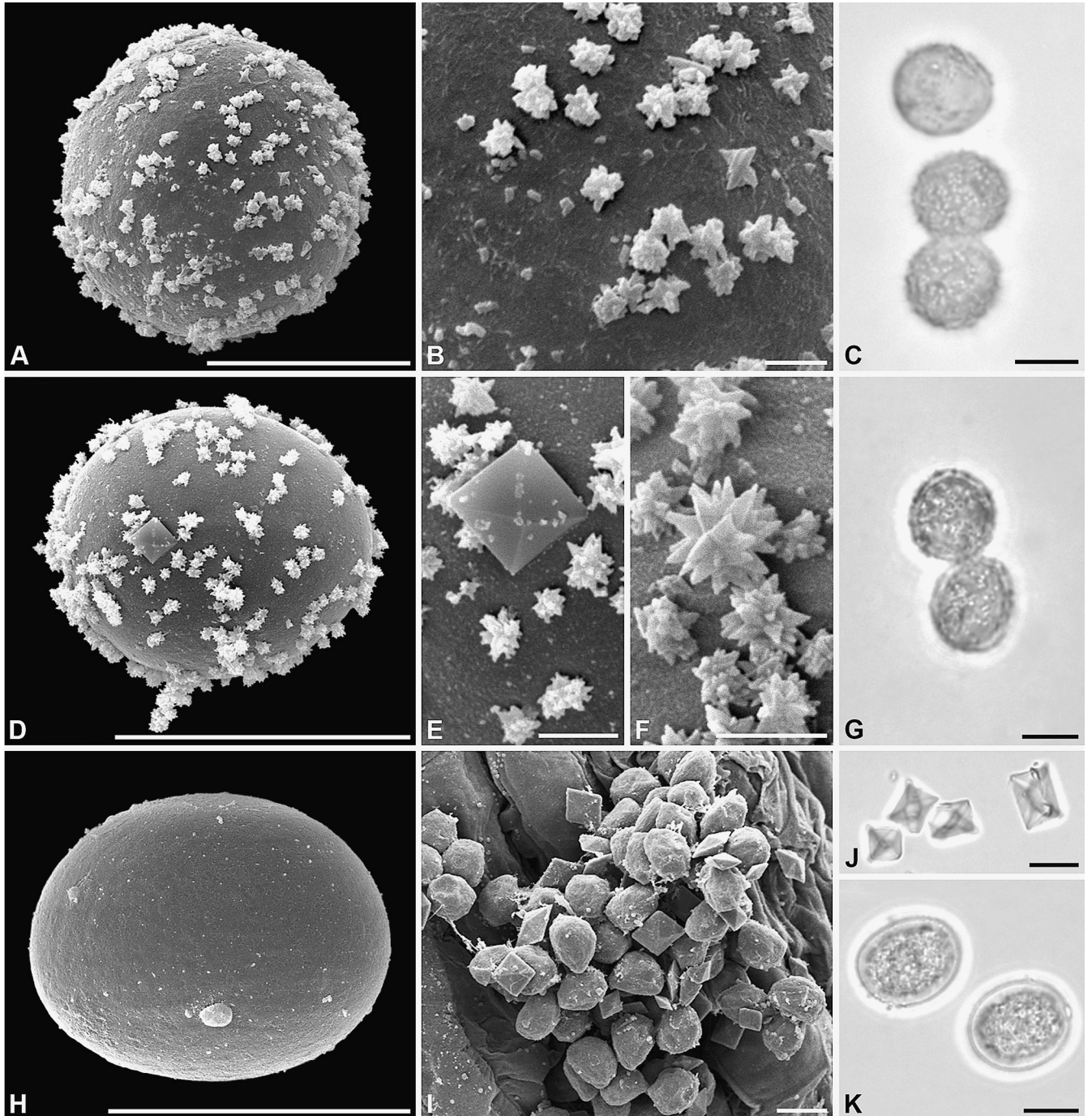

Fig. 2. Psilate pollen typical for *Schismatoglottis*. **A–C,** *Schismatoglottis celebica*: **A,** hydrated pollen grains under SEM, critical point–dried; **B,** detail of pollen surface; note the crystals covering the pollen surface; **C,** hydrated pollen grains under LM. **D–G,** *Schismatoglottis calyptrata*: **D,** hydrated pollen grains under SEM, critical point–dried; **E–F,** small and large crystals covering the pollen surface; **G,** hydrated pollen grains under LM; note crystals on the pollen surface. **H–K,** *Schismatoglottis multiflora*: **H,** hydrated pollen grains under SEM, critical point–dried: **I,** hydrated pollen grains under SEM, showing smooth pollen with large crystals attached, critical point–dried; **J,** crystals under LM; **K,** hydrated pollen grains under LM. — Scale bars = 10 µm (A, C, D, G, H–K), 1 µm (B, E, F).

layer stained electron-dense, but after treatment with potassium permanganate (Fig. 3E) and after the Lipid-test (Fig. 3G) it stained electron-lucent.

Spathe movements of _Apoballis acuminatissima_. — The inflorescence of _Apoballis acuminatissima_ consists of a fertile spadix surrounded by a spathe. The inflorescence is monoecious, with pistillate flowers at the base of the spadix, an intermediate sterile zone, staminate flowers above, and a terminal sterile zone, the appendix. In common with all Araceae _Apoballis_ is protogynous. In _Apoballis_ the pistillate flowers

are receptive during the first day of anthesis, and staminate flowers release pollen on the second day. During anthesis the inflorescence performs a series of movements (Fig. 4). Before onset of anthesis the spathe clings tightly to the spadix (Fig. 4A). Around 00:00 h of the first day the spadix bends forwards and the spathe limb starts to unfurl ventrally, finally completely exposing the sterile and staminate section of the spadix, and giving access to the pistillate flowers contained in the lower part of the spathe. Meanwhile, the tip of the spathe limb remains furled around the distal part of the spadix. The
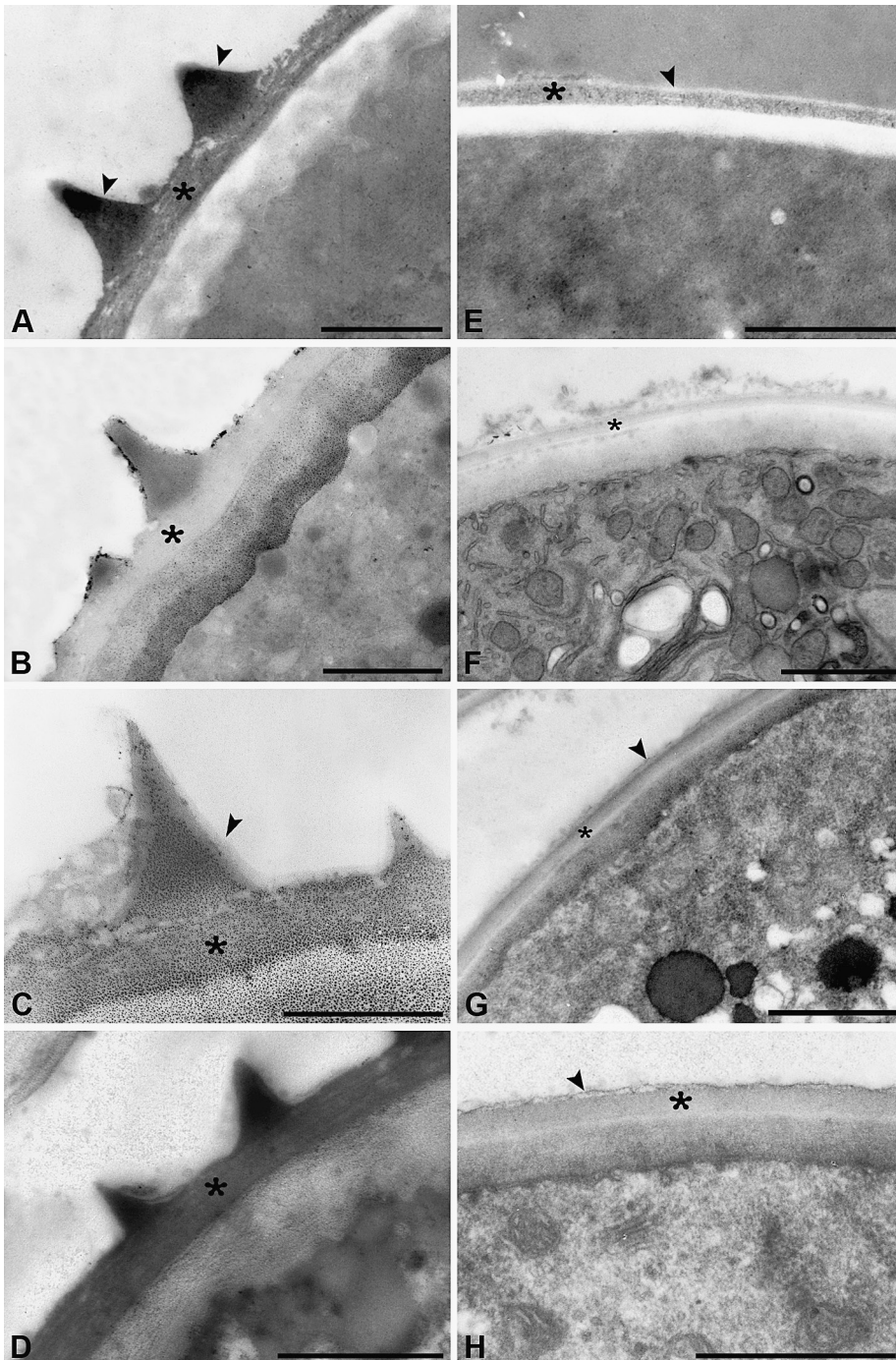
Fig. 3. Cross-sections of pollen walls of _Apoballis_ and _Schismatoglottis_ using different staining methods. **A–D,** _Apoballis acuminatissima_; **E–H,** _Schismatoglottis celebica_. **A, E,** pollen wall after potassium permanganate staining; **B, F,** pollen wall after modified Thiéry-test; **C, G,** pollen wall after Lipid-test; **D, H,** pollen wall after Thiéry-test. — Arrowheads point to a thin continuous layer, covering the pollen surface; asterisks indicate the endexine. Below the endexine a bi-layered intine is found. — Scale bars = 1 μm.

opening persists during the first day, throughout which the pistillate flowers are receptive. Maximum spathe limb opening is reached around 12:00 h of the first day (Fig. 4B). After 15:00 h the spadix bends back again and the spathe limb starts to close around the ventral part of the intermediate (sterile) zone of the spadix. By 04:00 h on the second day of anthesis the closing motion ends and the spathe tube enclosing the pistillate flowers is closed ventrally. The ventral side of the staminate zone of the spadix remains exposed while the dorsal side is enclosed by the spathe margins (Fig. 4C). After 14:30 h of the second day pollen is extruded from the staminate flowers (Fig. 4D). The staminate flowers on the dorsal side of the staminate zone extruded only a few pollen grains, while on the spathe-enclosed dorsal side more pollen was produced, which then fell into the spathe tube below. The moment of reopening of the spathe limb after the staminate phase differed in the observed plants. In two plants the spathe limb reopened on the same level with the staminate spadix zone two days after staminate anthesis (Fig. 4E) whereas in a third plant the

spathe limb remained closed until the inflorescence started to decay. As the upper part of the spathe limb remained furled throughout anthesis, the appendix was never exposed. After anthesis the spathe limb is marcescent (Fig. 4F).

■ DISCUSSION

Pollen characters of Araceae (ornamentation, ultrastructure) accord well with recent phylogenies and phylogeny-supported taxonomic accounts (Hay, 1996; Mayo & al., 1997; Hay & Yuzammi, 2000; Keating, 2002, 2004; Cabrera & al., 2008; Cusimano & al., 2011). One outcome of our current palynological research in Araceae is the almost absolute presence of psilate or verrucate pollen in all the earlier-diverging clades of Aroideae, including Schismatoglottideae (Cusimano & al., 2011). Until recently the monospecific genus *Callopsis* was the only example with echinate pollen within the earlier-diverging clades. Echinate pollen is typical for all more derived clades

Fig. 4. Spathe movements of *Apoballis acuminatissima*. **A,** pre-anthesis (1 day before anthesis); **B,** pistillate phase (day 1 of anthesis, 12:10 h), arrowhead indicates spathe opening; **C,** pre-staminate phase (day 2, 10:38 h); **D,** pollen shedding (day 2, 16:58 h), arrowheads indicate anthers releasing pollen; **E,** post-staminate phase (day 4, 11:23 h), arrowhead indicates spathe opening; **F,** withered inflorescence (day 9). — Scale bar = 2 cm.
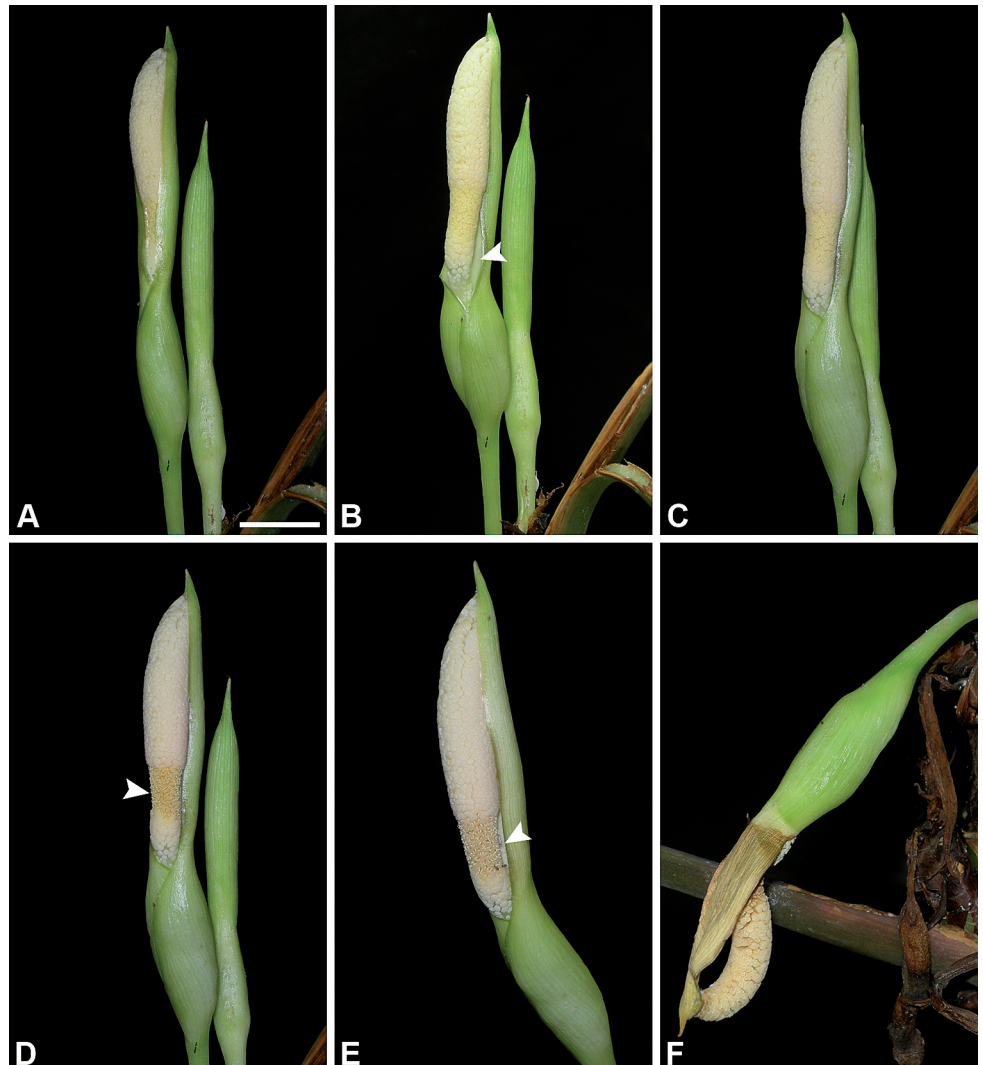
of Aroideae subfamily (Hesse, 2006; Halbritter, unpub. data), except for the genus *Amorphophallus* Blume ex Decne., where many different ornamentation types occur within a single genus (Van der Ham & al., 1998). Pollen of all *Schismatoglottis* species and species within the recently resurrected New World genus *Philonotion* Schott (Wong & al., 2010), so far studied by us (Appendix), is psilate, in accordance with literature reports (Grayum, 1992; Wong & al., 2011). Curiously Thanikaimoni (1969) reported 14 *Schismatoglottis* species with echinate (spiny) pollen, but only illustrated *Schismatoglottis kurzii* Hook. f. (= *Apoballis mutata* (Hook. f.) S.Y. Wong & P.C. Boyce), and *Schismatoglottis forbesii* Engl. (= *Apoballis longicaulis* (Ridl.) S.Y. Wong & P.C. Boyce). Unfortunately, Thanikaimoni's report was overlooked and even suspected as a misinterpretation of fungal spores (Grayum, 1992). The puzzling presence of a spiny-pollen *Schismatoglottis* species (the original *Schismatoglottis lancifolia*) in our collections, and the desire to verify or finally refute the largely ignored findings of Thanikaimoni (1969), were the reasons to undertake a close look at potentially spiny-pollen *Schismatoglottis* species.

Calcium crystals. — Under the light microscope, pollen of *Schismatoglottis celebica* and *Schismatoglottis calyptrata* appear to be echinate, but this is a misinterpretation. The scanning electron microscope reveals that irregularly distributed crystals of different size, not echini, cover the whole pollen surface. The smooth pollen surface of *Schismatoglottis multiflora* has no small crystals attached, but the pollen grains are clumped together with large crystals. Many aroids produce large amounts of oxalic acid and most of it is deposited as crystals of calcium (Mayo & al., 1997). A common feature of *Schismatoglottis* and some other Araceae (*Caladium* Vent., *Gearum* N.E. Br., *Scaphispatha* Brongn. ex Schott) is the occurrence of small and large calcium oxalate crystals attached to the pollen surface (Grayum, 1992; D'Arcy & al., 1996; Barabé & al., 2004).

Pollen analyses. — Pollen analyses under scanning and transmission electron microscope reveal that pollen of *Apoballis acuminatissima*, *A. longicaulis*, and *A. mutata*, is distinctively echinate. Because all species of *Apoballis* so far investigated have spiny pollen, a study of species of *Schismatoglottis* with *Apoballis*-like macromorphology should include pollen analyses. If their pollen is spiny and their morphology is as found in *Apoballis* then they should be transferred to *Apoballis*. If echinate pollen turns out to be common to all *Apoballis* species, it would be another fine example for the "compass needle" quality of pollen characters (Erdtman, 1952; Blackmore, 2000). In Schismatoglottideae, echinate pollen so far is restricted to *Apoballis*, the basalmost genus of the tribe (Wong & Boyce, 2010c).

Pollen wall. — The pollen wall of *Apoballis* and *Schismatoglottis* consists mainly of a thick, continuous spongy endexine overlaying a thick intine. A thin outermost layer is covering the endexine. The echini of *Apoballis* mainly consist of polysaccharides, which is a common feature of spiny pollen in Aroideae, and so far known only for Araceae (Weber & al., 1998, 1999). Although sporopollenin is absent, the spines of *Apoballis* are resistant to acetolysis. The use of different staining

methods revealed a thin outer pollen wall layer, covering the whole pollen surface. The echini are protected by this outer wall layer and therefore resistant to chemical attack. This is similar to *Callopsis volkensii* Engl., where the outer pollen wall layer was interpreted as a cuticula (Weber, 2004). Surprisingly, this outer wall layer stained electron-lucent or electron-dense depending on the staining method. This staining behaviour of a pollen wall layer is so far only known from the endexine. The results of the cytochemical reactions (Thiéry-test, Lipid-test, potassium permanganate) are in accordance with those reported in Weber & al. (1998) and as demonstrated for the staining behaviour of the endexine in Weber & Ulrich (2010). The staining results indicate that the chemical compounds of the outer wall layer might be similar to those of the endexine, which mainly consists of lipidic compounds, sporopollenin and proteins (Heslop-Harrison, 1968a, b; Heslop-Harrison & al., 1973). According to Weber (2004) the staining properties of the outer pollen wall layer of *Schismattoglottis* and *Apoballis* indicates lipidic compounds rather than sporopollenin and definitely no polysaccharides. Based on the staining results and the resistance to acetolysis, it seems more likely that this ektexine-like layer is a type of cuticula, This layer is unique for the tribe Schismattoglottideae, and for the Araceae so far only documented for *Callopsis* (Weber, 2004).

Pollen and pollinator. — Ornamented pollen (e.g., reticulate, echinate pollen) is significant for zoophily (Punt, 1986; Fægri & Iversen, 1989). Usually the ornamenting elements consist of sporopollenin, like the rest of the ektexine (Hesse, 2006). It is not understood if and how the non-sporopollenin (polysaccharidic) echini in *Apoballis*, and in many other members of Aroideae, are related to the mode of pollination.

Usually psilate pollen of temperate and boreal zones is indicative for anemophily (Fægri & Iversen, 1989), whereas in the tropics it is not indicative for anemophily, but for zoophily (Furness & Rudall, 1999). In Aroideae (e.g., *Montrichardia* Crueg., *Dieffenbachia* Schott, *Philodendron* Schott, *Gearum* N.E. Br.) psilate pollen, together with its sticky surface, is adapted for entomophily (Weber & Halbritter, 2007; our unpub. data). In Araceae, a correlation between pollinator type and pollen ornamentation is strongly suggested: beetle pollination is correlated with psilate pollen, fly pollination with echinate pollen (Grayum, 1992; Sannier & al., 2009). However, without pollinator observations for *Apoballis* it remains unclear whether there exists such a correlation in this genus, i.e., whether flies are the pollinators of *Apoballis*. According to the scarce literature (Toda & Lakim, 2011; Wong, Boyce & co-workers, pers. obs. & in prep.), at least some species of *Schismatoglottis* are pollinated by flies of the genus *Colocasiomyia* (Drosophilidae). This conflicts with the presence of smooth pollen grains which are interpreted as adaptation to beetle pollination. Moreover, the appearance of echinate pollen grains only in the derived clades of Aroideae (Cusimano & al., 2011) indicates a phylogenetic signal rather than an ecological trigger such as pollinator type.

Interestingly, all *Apoballis* so far investigated produce a floral odour reminiscent of benzaldehyde (almond oil; Boyce, pers. obs.) which contrasts with the floral odour of

Schismatoglottis (mainly methyl esterase-like—model airplane glue). This, together with the differences in spathe mechanics (Boyce & Wong, 2007), strongly suggests pollinator differences.

Spathe movements. — Variously complex spathe movements occur in all Schismatoglottideae species so far observed (Boyce & Wong, 2007; Wong & Boyce, 2010b), but to date no studies on the function of the movements have been published, although much data has been accumulated. In most genera, including *Schismatoglottis*, the spathe limb is caducous during or at the end of anthesis. This is not the case in *Apoballis*. In tribe Areae movements similar to those of *Apoballis* have been observed and published for *Typhonium* Schott, *Sauromatum* Schott, and *Theriophonum* Blume (Vogel, 1965; Armstrong, 1979; Dakwale & Bhatnagar, 1997). In these genera, spathe movements serve as trapping mechanisms for flies as well as beetles that would otherwise escape from the lower spathe tube before pollen is extruded. In these taxa insects are arrested in the lower spathe tube containing the pistillate flowers until pollen is extruded from the staminate flowers above the secluded chamber and deposited onto the constriction that separates the lower spathe and the spathe limb. When the constriction loosens insects escape with pollen attached to their bodies. The crucial event in *Apoballis acuminatissima* is the locking of the spathe tube during the pistillate phase; we hypothesize that the primary purpose of these spathe movements is to arrest pollinators in order to exploit them as pollen vectors during the staminate phase. In contrast to *Typhonium*, *Sauromatum* and *Theriophonum*, part of the staminate section is situated inside the secluded chamber and thus pollen directly falls into the lower spathe tube. Two scenarios seem possible: trapped insects take up pollen during their arrestment within the spathe tube, or when they leave the spathe tube through the narrow opening on a level with the staminate flowers. In effect spathe movements, and changes in spadix morphology during anthesis function as "pollinator management systems". Such a mechanism can greatly increase reproductive success (Lack & Diaz, 1991). The observation that traps are more often found among fly-pollinated Araceae (Bown, 2000) would indicate flies as pollinators in *Apoballis* rather than beetles. Whether or not differences in spathe movements between *Apoballis* and *Schismatoglottis* are owing to different types of pollinators needs further investigation.

Compared to the trapping species of Areae, where insects are released immediately after pollen production, the two days delay before the reopening of the spathe in *Apoballis* might seem atypical. However, exceptions to the rule exist. For example, in *Arum hygrophilum* Boiss. times of arrestment of up to 10 days have been recorded (Koach, 1985). The fact that the moment of reopening differed in inflorescences of the same plant indicates certain variability. However, more observations on different plants, ideally in their natural habitat with pollinators present, are necessary to understand the function of the delayed opening. The reversible bending of the spadix as part of the spathe movements reveals a high degree of synorganisation of the inflorescence. It is a unique feature of *Apoballis* which has not been observed yet in any other taxon of Araceae.

■ CONCLUSION

In this paper, we provide another compelling example for the "compass needle" quality of pollen characters: it indicates that spiny pollen in the genus *Apoballis* is plesiomorphic for Schismatoglottideae, while pollen in *Schismatoglottis* (and indeed all other studied Schismatoglottideae) is psilate. The echinate pollen of *Apoballis* may indicate different types of pollinators. A specialized relationship between plant and pollinator is indicated by the spathe movements in *Apoballis*, which clearly differ from those in *Schismatoglottis*. The observed traits would indicate flies as pollinators. To clarify this issue field studies are needed. Moreover, we recommend further pollen studies of *Schismatoglottis* species with *Apoballis*-like macromorphology.

■ LITERATURE CITED

Agar Scientific Limited. 2004. Technical note—information on LV-Resin. www.agarscientific.com.

Armstrong, J.A. 1979. Biotic pollination mechanisms in the Australian flora—a review. *New Zealand J. Bot.* 17: 467–508.

Barabé, D., Lacroix, C. & Gibernau, M. 2004. Aspects of floral morphology in *Ambrosina* and *Arisarum* (Araceae). *Canad. J. Bot.* 82: 282–289.

Blackmore, S. 2000. The palynological compass: The contribution of palynology to systematics. Pp. 161–177 in: Nordenstam, B., El-Ghazaly, G. & Kassas, M. (eds.), *Plant systematics for the 21st century*. London: Portland Press.

Bown, D. 2000. *Aroids: Plants of the* Arum *family*. Portland: Timber Press.

Boyce, P.C. & Wong, S.Y. 2007. Studies on Schismatoglottideae (Araceae) of Borneo IV: Preliminary observations of spathe senescence mechanics in *Schismatoglottis* Zoll. & Moritzi, in Sarawak, Malaysian Borneo. *Aroideana* 30: 56–70.

Cabrera, L.I., Gerardo, A.S., Chase, M.W., Mayo, S.J., Bogner, J. & Dávila, P. 2008. Phylogenetic relationships of aroids and duckweeds (Araceae) inferred from coding and noncoding plastid DNA. *Amer. J. Bot.* 95: 1153–1165.

Cusimano, N., Bogner, J., Mayo, S.J., Boyce, P.C., Wong, S.Y., Hesse, M., Hetterscheid, W.L.A., Keating, R.C. & French, J.C. 2011. Relationships within the Araceae: Comparison of morphological patterns with molecular phylogenies. *Amer. J. Bot.* 98: 654–668.

Dakwale, S.R. & Bhatnagar, S. 1997. Midge-trapping behaviour and floral biology of *Theriophonum crenatum* Blume. Rumph. (Araceae). *Curr. Sci.* 73: 607–608.

D'Arcy, W.G., Keating, R.C. & Buchmann, S.L. 1996. The calcium

oxalate package or so-called resorption tissue in some angiosperm anthers. Pp. 159–190 in: D'Arcy, W.G. & Keating, R.C. (eds.), *The anther: Form, function and phylogeny*. Cambridge: Cambridge University Press.

Erdtman, G. 1952. *Pollen morphology and plant taxonomy: Angiosperms*. Stockholm: Almqvist & Wiksell.

Erdtman, G. 1960. The acetolysis method: A revised description. *Svensk Bot. Tidskr.* 54: 561–564.

Fægri, K. & Iversen, J. 1989. *Textbook of pollen analysis*, 4th ed. Chichester: John Wiley & Sons.

French, J.C., Chung, M. & Hur, Y. 1995. Chloroplast DNA phylogeny of the Ariflorae. Pp. 255–275 in: Rudall, P.J., Cribb, P.J., Cutler, D.F. & Humphries, C.J. (eds.), *Monocotyledons: Systematics and evolution*. Kew: Royal Botanic Gardens.

Furness, C.A. & Rudall, P.J. 1999. Inaperturate pollen in monocotyledons. *Int. J. Pl. Sci.* 160: 395–414.

Grayum, M.H. 1986. Correlations between pollination biology and pollen morphology in the Araceae, with some implications for angiosperm evolution. Pp. 313–327 in: Blackmore, S. & Ferguson, I.K. (eds.), *Pollen and spores: Form and function*. New York, London: Academic Press.

Grayum, M.H. 1992. Comparative external pollen ultrastructure of the Araceae and putatively related taxa. *Monogr. Syst. Bot.* 43: 1–167.

Halbritter, H. 1998. Preparing living pollen material for scanning electron microscopy using 2,2-Dimethoxypropane (DMP) and critical-point drying. *Biotechnic Histochem.* 73: 137–143.

Hay, A. 1996. The genus *Schismatoglottis* Zoll. & Moritzi (Araceae–Schismatoglottideae) in Peninsular Malaysia and Singapore. *Sandakania* 7: 1–30.

Hay, A. & Yuzammi. 2000. Schismatoglottideae (Araceae) in Malesia I—*Schismatoglottis. Telopea* 9: 1–177.

Hayat, M.A. 2000. *Principles and techniques of electron microscopy: Biological applications.* Cambridge: Cambridge University Press.

Heslop-Harrison, J. 1968a. Pollen wall development. *Science* 161: 230–237.

Heslop-Harrison, J. 1968b. Tapetal origin of pollen coat substances in *Lilium. New Phytol.* 67: 779–786.

Heslop-Harrison, J., Heslop-Harrison, Y., Knox, R.B. & Howlett, B. 1973. Pollen-wall proteins: 'gametophytic' and 'sporophytic' fractions in the pollen walls of the Malvaceae. *Ann. Bot.* 37: 403–412.

Hesse, M. 2006. Pollen wall ultrastructure of Araceae and Lemnaceae in relation to molecular classifications. *Aliso* 22: 204–208.

Hesse, M. & Waha, M. 1989. A new look at the acetolysis method. *Pl. Syst. Evol.* 163: 147–152.

Keating, R.C. 2002. *Acoraceae and Araceae.* Vol. 9 of: Gregory, M. & Cutler, D.F. (eds.), *Anatomy of the monocotyledons.* Oxford, U.K.: Clarendon Press.

Keating, R.C. 2004. Vegetative anatomical data and its relation to a revised classification of the genera of Araceae. *Ann. Missouri Bot. Gard.* 91: 485–494.

Koach, J. 1985. *Bio-ecological studies of flowering and pollination in Israeli Araceae.* Ph.D. thesis, University of Tel-Aviv, Israel. [in Hebrew with English abstract]

Lack, A.J. & Diaz, A. 1991. The pollination of *Arum maculatum* L.—A historical review and new observations. *Watsonia* 18: 333–342.

Mayo, S.J., Bogner, J. & Boyce, P.C. 1997. *The genera of Araceae.* Kew: The Trustees, Royal Botanic Gardens.

Ørgaard, M. & Jacobsen, N. 1998. SEM study of surface structures of the spathe in *Cryptocoryne* and *Lagenandra* (Araceae: Aroideae: Cryptocoryneae). *Bot. J. Linn. Soc.* 126: 261–289.

Pacini, E. & Juniper, B.E. 1983. The ultrastructure of the formation and development of the amoeboid tapetum in *Arum italicum* Miller. *Protoplasma* 117: 116–129.

Punt, W. 1986. Functional factors influencing pollen form. Pp. 313–327 in: Blackmore, S. & Ferguson, I.K. (eds.), *Pollen and spores: Form and function.* New York, London: Academic Press.

Rowley, J.R. & Dahl, A.O. 1977. Pollen development in *Artemisia vulgaris* with special reference to glycocalyx material. *Pollen & Spores* 19: 169–284.

Sannier, J., Baker, W.J., Anstett, M.C. & Nadot, S. 2009. A comparative analysis of pollinator type and pollen ornamentation in the Araceae and the Arecaceae, two unrelated families of the monocots. *B. M. C. Res. Notes* 2: 145, doi:10.1186/1756-055-2-145.

Spurr, A.R. 1969. A low-viscosity epoxy resin embedding medium for electron microscopy. *J. Ultrastruct. Res.* 26: 31–43.

Thanikaimoni, G. 1969. Esquisse palynologique des Aracées. *Trav. Sect. Sci. Techn. Inst. Franç. Pondichéry* 5: 1–31.

Thiéry, J.P. 1967. Mise en évidence des polysaccharides sur coupes fines en microscope électronique. *J. Microscopie* 6: 987–1018.

Toda, M.J. & Lakim, M.B. 2011. Genus *Colocasiomyia* (Drosophilidae: Diptera) in Sabah, Bornean, Malaysia: High species diversity and use of host aroid inflorescences. *J. Entomol. Sci.* 14: 262–270.

Ulrich, S. 2006. *Pollenmorphologie und Ultrastruktur ausgewählter Lamianae.* Diploma thesis, University of Vienna, Austria.

Van der Ham, R.W.J.M., Hetterscheid, W.L.A. & Van Heuven, B.J. 1998. Notes on the genus *Amorphophallus* (Araceae)—8: Pollen morphology of *Amorphophallus* and *Pseudodracontium. Rev. Paleobot. Palynol.* 103: 95–142.

Vogel, S. 1965. Kesselfallen-Blumen. *Umschau Wiss. Techn.* 65(1): 12–17.

Vogel, S. & Martens, J. 2000. A survey of the function of the lethal kettle traps of *Arisaema* (Araceae), with records of pollinating fungus gnats from Nepal. *Bot. J. Linn. Soc.* 133: 61–100.

Weber, M. 2004. Unique pollen features in Araceae [Abstract, XI International Palynological Congress. Granada]. *Polen* 14: 18.

Weber, M. & Halbritter, H. 2007. Exploding pollen in *Montrichardia arborescens* (Araceae). *Pl. Syst. Evol.* 263: 51–57.

Weber, M. & Ulrich, S. 2010 The endexine: A frequently overlooked pollen wall layer and a simple method for detection. *Grana* 49: 83–90.

Weber, M., Halbritter, H. & Hesse, M. 1998. The spiny pollen wall in *Sauromatum* (Araceae)—with special reference to the endexine. *Int. J. Pl. Sci.* 159: 744–749.

Weber, M., Halbritter, H. & Hesse, M. 1999. The basic pollen wall types in Araceae. *Int. J. Pl. Sci.* 160: 415–423.

Wong, S.Y. & Boyce, P.C. 2010a. Studies on Schismatoglottideae (Araceae) of Borneo IX: A new genus, *Hestia*, and resurrection of *Apoballis. Bot. Stud. (Teipei)* 51: 249–255.

Wong, S.Y. & Boyce, P.C. 2010b. Studies on Schismatoglottideae (Araceae) of Borneo X. *Pichinia*, a new genus from Sarawak, Malaysian Borneo. *Gard. Bull. Singapore* 61: 541–548.

Wong, S.Y. & Boyce, P.C. 2010c. Studies on Schismatoglottideae (Araceae) of Borneo XI: *Ooia*, a new genus, and a new generic delimitation for *Piptospatha. Bot. Stud. (Teipei)* 51: 543–552.

Wong, S.Y., Bogner, J. & Boyce, P.C. 2011. A new endemic species of *Schismatoglottis* (Araceae) from the Philippines. *Willdenowia* 41: 101–106.

Wong, S.Y., Boyce, P.C., bin Othman, A.S. & Pin, L.C. 2010. Molecular phylogeny of tribe Schismatoglottideae (Araceae) based on two plastid markers and recognition of a new tribe, Philonotieae, from the neotropics. *Taxon* 59: 117–124.

Young, H.J. 1986. Beetle pollination of *Dieffenbachia longispatha* (Araceae). *Amer. J. Bot.* 73: 931–944.

Zavada, M.S. 1983. Comparative morphology of monocot pollen and evolutionary trends of apertures and wall structures. *Bot. Rev. (Lancaster)* 49: 331–379.

Appendix. Species sampled. Specimens where collected in Malaysia, from Munich Botanical Garden, and from the Botanical Garden of the University of Vienna.

Species, locality, collector (herbarium/voucher).

Apoballis Schott: *A. acuminatissima* (Schott) S.Y. Wong & P.C. Boyce, cult. Botanical Garden of the University of Vienna, *J. Bogner 1797, Anon. s.n.*, (090609-1/2); *A. mutata* (Scort. ex Hook.f.) S.Y. Wong & P.C. Boyce, Malaysia, Perak, Hulu Perak, Tasik Banding, cult. USM Penang, ex *Baharuddin S. s.n.* sub. *P.C. Boyce & S.Y. Wong AR-2616* (SAR, USM). *Bucephalandra* Schott: *B. motleyana* Schott, cult. Munich Botanical Garden, *J. Bogner 2974* (M). *Hestia* S.Y. Wong & P.C. Boyce: *H. longifolia* (Ridl.) S.Y. Wong & P.C. Boyce, Malaysia, Sarawak, Kuching, Bau, Kampung Grogo, *Jeland ak. Kisai AR-233* (SAR). *Schismatoglottis* Zoll. & Moritzi: *S. calyptrata* (Roxb.) Zoll. & Moritzi, Malaysia, Perak Hulu, Perak, Tasik Banding, cult. USM Penang, *Baharuddin S. s.n.* sub. *P.C. Boyce & S.Y. Wong AR-2617* (SAR, USM); *S. calyptrata*, cult. Botanical Garden of the University of Vienna [ARA090165] ex *J. Bogner s.n.* (090402-1/1); *S. celebica* Engl., Indonesia, Sulawesi, cult. Botanical Garden of University Vienna [ARA090160], ex *Chr. Kasselmann s.n.*; *S. conoidea* Engl., Malaysia, Sarawak, Kuching, Matang, Kubah N.P., Waterfall Trail, 01°35′40.2″N, 110°10′45.9″E, 190 m asl, *P.C. Boyce & S.Y. Wong AR-2113* (SAR); *S. ifugaoensis* S.Y. Wong, Bogner & P.C. Boyce, Philippines, Luzon, Ifugao Province, near Banaue, ca. 1500 m asl, *J. Bogner 1630* (M); *S. matangensis* S.Y. Wong, Malaysia, Sarawak, Kuching, Matang, Kubah N.P., Waterfall Trail, 01°35′40.2″N, 110°10′45.9″E, 190 m asl, *P.C. Boyce & Wong Sin Yeng, AR-1864* (SAR); *S. modesta* Schott, Indonesia, Kalimantan Barat, Sanggau, Kampung Penyeladi between Sekadau and Sanggau, 00°05′00.1″N, 110°39′54.8″E, *P.C. Boyce & S.Y. Wong AR-2547* (BO, SAR); *S. motleyana* (Schott) Engl., Malaysia, Sarawak, Kuching, Matang, Kubah N.P., Waterfall Trail, 01°35′40.2″N, 110°10′45.9″E, 190 m asl, *P.C. Boyce, Wong Sin Yeng & S. Maclean AR-2116* (SAR); *S. multiflora* Ridl., Malaysia, Sarawak, Kuching, Matang, Kubah N.P. boundary, Sungai Cina, cult. Botanical Garden of the University of Vienna, [ARA090167], *J. Bogner 1453*, (091027-1/1); *S. roseospatha* Bogner, Malaysia, Sarawak, Kapit, Gaat ('Gaad') River, *J. Knüppel & H. Link s.n.*, cult. Munich Botanical Garden sub. *J. Bogner 1472* (M); *S. tecturata* (Schott) Engl., Malaysia, Sarawak, Kapit, Kapit town, Taman Rekreasi Sebabai, 01°56′45.6″N, 112°54′16.8″E, ca. 50 m asl, *P.C. Boyce, Wong Sin Yeng & Jeland ak Kisai AR-1797* (SAR); *S. viridissima* A. Hay, Malaysia, Sarawak, Kuching, Matang, Kubah N.P., Waterfall Trail, 01°35′40.2″N, 110°10′45.9″E, 190 m asl, *P.C. Boyce, Wong Sin Yeng & S. Maclean AR-2126* (SAR). *Ooia* S.Y. Wong & P.C. Boyce: *O. grabowskii* (Engl.) S.Y. Wong & P.C. Boyce, Malaysia, Sarawak, Kapit, Kapit town, Taman Rekreasi Sebabai, 01°56′45.6″N, 112°54′16.8″E, ca. 50 m asl, *P.C. Boyce & Wong Sin Yeng AR-2430* (SAR). *Philonotion* Schott: *P. spruceanum* Schott, Venezuela, Amazonas, 1°53′N, 67°02′E, cult. Munich Botanical Garden, *J. Bogner, G. Davidse, J.S. Miller 26477* (M). *Phymatarum* M. Hotta: *P. borneense* M. Hotta, Malaysia, Sarawak, Miri, Marudi, Long Lama, Mulu N.P., trail to Deer Cave, 04°02′23.8″N, 114°48′54.6″E, ca. 60 m asl, *Low Shook Ling 3* (SAR). *Piptospatha* N.E. Br.: *P. ridleyi* N.E.Br. ex Hook.f., cult. Munich Botanical Garden, *J. Bogner 1270* (M); *P. viridistigma* S.Y. Wong, P.C. Boyce & Bogner, Malaysia, Sarawak, Samarahan, Serian, Taman Rekreasi Ranchan, 01°08′34.9″N, 110°35′02.4″E, ca. 55 m asl, *P.C. Boyce & Wong Sin Yeng AR-2432* (SAR). *Schottariella* P.C. Boyce & S.Y. Wong: *S. mirifica* P.C. Boyce & S.Y. Wong, Malaysia, Sarawak, Sarikei, Maradong, Sungai Matob, 01°52′06.1″N, 111°55′30.7″E, ca. 55 m asl, *P.C. Boyce & al. AR-1615* (SAR).