Studies on Schismatoglottideae (Araceae) of Borneo IV: Preliminary Observations of Spathe Senescence Mechanics in *Schismatoglottis* Zoll. & Moritzi in Sarawak, Malaysian Borneo

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ABSTRACT

Recent alpha-taxonomic studies of *Schismatoglottis* Zoll. & Moritzi provide a sufficiently stable framework to facilitate taxonomically robust multidisciplinary research, notably molecular phylogenetic, ecological and phenological studies including analyses of morphological adaptations to specialized ecology (in particular rheophytism), and comparison of mechanical processes linked to pollination strategies (notably spathe senescence). Such data will later be mapped onto molecular-generated phylogenetic trees in order to analyse their origins. The various processes by which the spathe limb is shed during or post anthesis is the subject here of a preliminary discussion. The significance of these data is reviewed in terms of the currently proposed informal infrageneric groupings.

KEY WORDS

Schismatoglottis, Schismatoglottideae, spathe limb senescence mechanics, Malaysia, Sarawak, Borneo, Araceae.

INTRODUCTION

Schismatoglottis Zoll. & Moritzi is a predominantly Palaeotropical genus (type [*S. calyptrata* (Roxb.) Zoll & Moritzi tropical Asian]; generic status of the three described Neotropical species yet to be phylogenetically tested) of more than of 100 species of terrestrial herbaceous mesophytes, less often rheophytes, very rarely helophytes, with a primary distribution centred on Borneo. In recent years *Schismatoglottis* has been the subject of a major alpha-taxonomic revision (Hay & Yuzammi, 2000) which, together with subsidiary papers describing additional Bornean novelties (Hay, 2002; Hay & Herscovitch, 2003; Boyce & Wong, 2007; Wong, 2007; Wong & Boyce, 2007), and with the caveat that numerous tropical Asian novelties remain yet to be described, provides an alpha-taxonomy sufficiently stable to facilitate higher level (molecular phylogenetic) and multidisciplinary (notably ecological and phenological) studies.

Inflorescence Morphology and Spathe Senescence Mechanics in *Schismatoglottis*

The generic name *Schismatoglottis* is from the Greek *schisma, schismatos* (separating) and *glôtta* (tongue) and refers to the usually deciduous spathe limb that is a feature of most species.

Hay & Yuzammi (2000) provided a preliminary overview of spathe limb senescence

Table 1. Informal groups for *Schismatoglottis* as proposed by Hay & Yuzammi (2000) with additional notes in square brackets.

Informal Group after Hay & Yuzammi (2000)	Spathe Characters	Vegetative & Other Characters
corneri	Spathe limb hardly opening and semi-persistent	Shoot pleionanthic; leaf sheath fully attached. Inflorescence pendulous. Not rheophytic
rupestris	Spathe usually hardly opening and semi-persistent.	Shoot pleionanthic; leaf sheath long, developing fully attached, then usually deciduous; interstice of spadix prominent, mostly naked with a few groups of small more or less sessile staminodes. Occasionally rheophytic.
asperata	Spathe inflating and limb gaping at female anthesis and then opening more or less wide at male anthesis before shedding though crumbling-deliquescing [some exceptions]	Shoot pleionanthic; leaf sheath nearly always fully attached and persistent. Rarely rheophytic.
multiflora	Spathe limb caducous [some exceptions]	Shoot pleionanthic; leaf sheath free-ligular. Spadix often held subhorizontal (apex of peduncle and/or base of female zone bent); appendix sometimes absent. Often rheophytic.
calyptrata	Spathe limb caducous [numerous exceptions]	Shoot usually hapaxanthic; leaf sheath fully attached and persistent. Appendix rarely absent. Sometimes rheophytic
tecturata	Spathe limb persistent/ marcescent or caducous.	Shoot pleionanthic; leaf sheath very short and fully attached; foliage leaves alternating with prophylls or cataphylls; spadix erect. Sometimes rheophytic.

mechanics which, together with petiolar sheath and shoot architecture characters, formed the basis of the six informal groups they proposed for Malesian *Schismatoglottis* (Table 1).

In its typical form the spathe in *Schismatoglottis* is differentiated into a lower persistent portion enclosing the female zone of the spadix and an upper ephemeral spathe limb subtending the male zone and appendix. The point of differentiation is usually marked by a constriction. In some species this constriction loosens at female anthesis, allowing access to pollinators. However, in many species it is the whole lower spathe that loosens, providing a narrow opening at the overlap of the convolution through which visitors gain access to the spadix, while the constriction remains tight until

after female anthesis, and then, before male anthesis, loosens to allow insects trapped in the lower spathe to ascend the spadix or spathe interior to gain access to pollen and eventually exit the inflorescence.

Hay & Yuzammi's speculation that the loosening and tightening of the constriction is to prevent self-pollen falling into the lower spathe chamber is improbable since, in all species we have so far observed, by the time pollen is released the stigmas are no longer receptive. It seems more likely that the various movements of the spathe are associated with pollinator management; trapping and releasing insects as the various parts of the spadix function.

Hay & Yuzammi (2000) noted that at female anthesis the spathe limb is usually inflated and gapes (listing exceptions, e.g., *S. elegans* A. Hay which opens wide and reflexes and *S. rupestris* Zoll. & Moritzi in which, with immediate allies, together with the unrelated *S. corneri* A. Hay, and *S. longifolia* Ridl. the limb hardly opens at all.)

We have observed that there is considerable variation in the spathe mechanics at female anthesis, and that the inflation and/or expanding of the spathe limb seems to be closely linked to the interfertile phase between the completion of the female flower function (receptivity) and the onset of pollen release, and that in many species the spathe limb remains quite tightly furled before pollen release.

Corneri Group

Schismatoglottis corneri (the sole species in the group and, to date, not recorded in Sarawak) has the limb persistent until after anthesis and then gradually degrading and falling while still clasping the spent parts of the spadix. As yet no further observations have been made.

Rupestris Group

In species allied to *S. rupestris* the spathe limb persists after anthesis before gradually degrading and falling while still clasping the spent parts of the spadix. The Rupestris Group is supposedly absent from Borneo, but the authors' work on several undescribed species suggests that the group may be present in central Sarawak although as yet no further observations have been made.

Asperata Group

It is this group that shows the most variation in spathe senescence mechanics, although all species so far studied are notable for the open-topped (not closely constricted) persistent lower spathe during the maturation of the fruits (Fig. 1). Bogner & Hay (2000) alluded to the similarity of the fruiting phase lower spathe in the *elongata* Group of the satellite genus *Piptospatha* N. E. Br. although in that genus the salver-shaped, persistent lower spathe is leathery and does not split to release the fruits, as is the situation in *S. asperata*, but rather appears to function as a splash cup.

Species most closely allied to *S. asperata* Engl. sensu Hay & Yuzammi have the spathe inflating and the limb gaping at female anthesis, then opening more or less wide at male anthesis before shedding, though crumbling-deliquescing; typical of this are *S. asperata* and *S. jelandii* P. C. Boyce & S. Y. Wong (Figs. 2 & 3).

Species of the complex around *S. multinervia* have a thick-textured spathe limb that is green outside and dark coloured and deeply glossy internally. The spathe limb inflates and gapes slightly at female anthesis and then, at the onset of male anthesis, splits longitudinally into two or more strips that reflex to reveal the spadix appendix; the complex is here typified by *S. multinervia* (Figs. 4 & 5). So far as is known, species in the *multinervia* complex are restricted to limestone and are all locally endemic: *S. multinervia* to Mulu. *Schismatoglottis puberulipes* Alderw. is perhaps allied to the *multinervia* complex, although the spathe limb is white and rather soft textured and abscises in a single piece (Figs. 6, 7 & 8).

Species of the *S. patentinervia* complex are striking not only for their distinctive

Fig. 1. *Schismatoglottis asperata* Engl. infructescence at early fruiting stage showing the open persistent lower spathe.

erect shoots with lorate leaf laminae borne on broadly winged petioles, but also by the inflorescences carried deep within the shoot tips (Fig. 9). Female flower receptivity is marked by the spathe inflating and the spathe limb gaping slightly. During male anthesis the spathe limb opens somewhat further before senescing in a way similar to that of *S. clarae* A. Hay (Calyptrata Group) with the spathe limb liquefying. However, species in the *patentinervia* complex differ from *S. clarae* by the liquefied limb subsequently drying onto the spadix and shedding when the post-anthetic upper spadix is shed (Fig. 10).

The *S. nervosa* complex is particularly interesting in that all species are strongly aromatic when crushed, a feature more often associated with *Homalomena* Schott (Homalomeneae). Hay & Yuzammi (2000) recognized two species (*S. nervosa* Ridl. & *S. elegans* A. Hay) although work by the second author suggests that there are several additional novelties awaiting formal recognition (Wong, in prep.) Aside from the distinctive tissue smell (and presumably distinctive biochemistry) the *nervosa* complex is notable for the manner in which the spathe limb is shed. In almost all species studied to date after an initial inflating and gaping phase coinciding with female anthesis the spathe limb liquefies into a mucilaginous mess without first breaking into pieces (Figs. 11 & 12). One exception to this is an as yet undetermined species from the granites of NW Sarawak (Fig. 13) in which the spathe limb fragments into irregular pieces as it is shed.

Species allied to *S. conoidea* Engl., aside from distinctive elongated shoot internodes giving rise to plants with a straggling habit, have the spathe limb hardly opening and long persistent into male anthesis, before shedding in pieces. The spathe is also

Fig. 2. *Schismatoglottis jelandii* P. C. Boyce & S. Y. Wong. Right hand inflorescence at early male anthesis; note wide open spathe limb.

Fig. 3. *Schismatoglottis jelandii* P. C. Boyce & S. Y. Wong. Left hand inflorescence at end of male anthesis; note beginning to deliquesce.

Fig. 4. *Schismatoglottis multinervia* M. Hotta at female anthesis; note slightly inflated and gaping spathe limb.

Fig. 5. *Schismatoglottis multinervia* M. Hotta at the onset of male anthesis; note that the discolorous spathe limb splits longitudinally into two or more strips that reflex to reveal the spadix appendix.

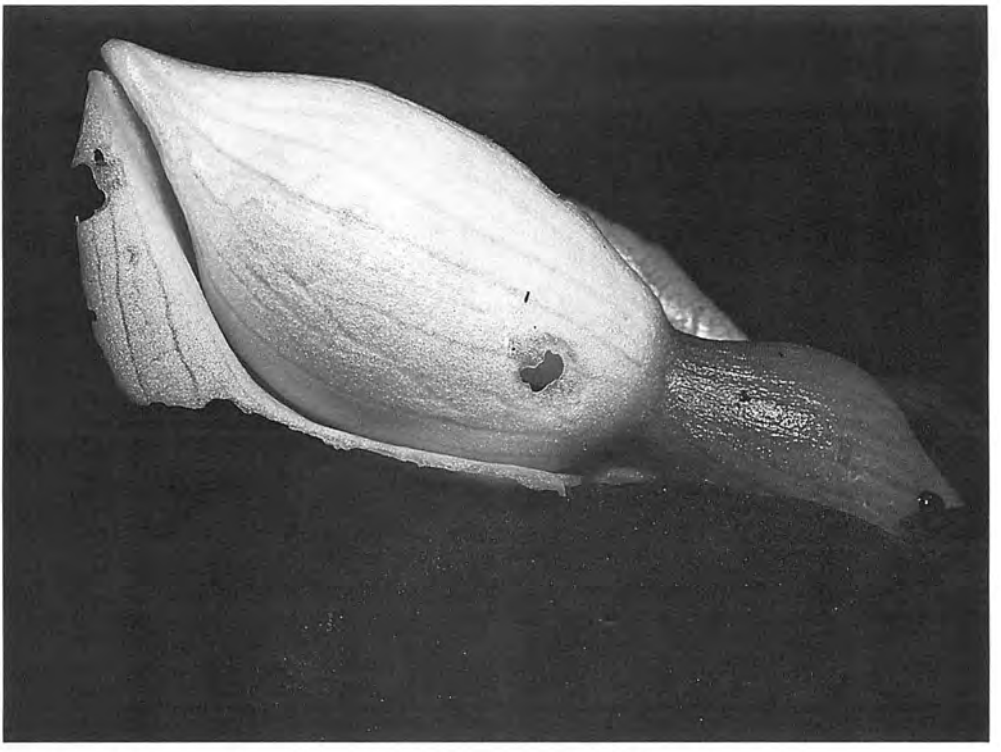

Fig. 6. *Schismatoglottis puberulipes* Alderw. at late female anthesis.

Fig. 7. *Schismatoglottis puberulipes* Alderw. at early male anthesis; note the abscission just beginning.

Fig. 8. *Schismatoglottis puberulipes* Alderw. at late male anthesis; spathe limb now almost fully detached but still intact.

Fig. 9. *Schismatoglottis* sp. aff. *patentinervia* Engl. at early male anthesis.

Fig. 10. *Schismatoglottis* sp. aff. *patentinervia* Engl. at late male anthesis; the spathe limb has deliquesced and is now drying onto the spadix.

Fig. 11. *Schismatoglottis nervosa* Ridl. at the post-female/pre-male anthesis interval; note the intact spathe limb beginning to deliquesce.

Fig. 12. *Schismatoglottis nervosa* Ridl. at the post-male anthesis; spathe limb completely melted and shed.

Fig. 13. *Schismatoglottis* sp. aff. *nervosa* Ridl. from granites; note the spathe limb breaking into irregular pieces as it is shed.

notably thick and glossy (Fig. 14) as opposed to the rather spongy texture of species closely allied to *S. asperata*.

The diversity of the Asperata Group sensu Hay & Yuzammi (notably the species complexes of *S. multinervia* and *S patentinervia*) combined with distinctive vegetative morphologies and indications of peculiar biochemistry (i.e., elongated internodes in the *conoidea* complex and aromatic tissues in the *nervosa* complex) suggest that the Asperata Group may be heterogeneous.

Multiflora Group

The Multiflora Group is defined vegetatively by pleionanthic shoots with the greater proportion of the petiolar sheath free-ligular and usually (but not exclusively) marcescent-deciduous and the spathe limb caducous and falling in a single piece. Typical of the group is *S. mayoana* Bogner & M. Hotta (Fig. 15), endemic to the Matang massif.

While the majority of the species in the Multiflora Group we have observed

Fig. 14. *Schismatoglottis conoidea* Engl. at late female anthesis.

Fig. 15. *Schismatoglottis mayoana* Bogner & M. Hotta; typical of the Multiflora group by the spathe limb caducous and falling in a single piece.

Fig. 16. *Schismatoglottis multiflora* Ridl. has a spathe limb persistent into the late stage of anthesis (left hand inflorescence is at the post-female/pre-male anthesis interval).

Fig. 17. An atypical species in the Multiflora group, as yet undescribed, in which the inflorescence has the spathe limb irregularly crumbling.

Fig. 18. *Schismatoglottis calyptrata* (Roxb.) Zoll. & Moritzi and its immediate allies are notable for the spathe limb caducous just prior to male anthesis, abscising cleanly at the top of the lower spathe and falling in a single piece.

follow the description of spathe mechanics given above, *S. multiflora* Ridl. (Fig. 16) has a spathe limb persistent into the late stage of anthesis and also employs a series of spathe movements so far unique for the genus and seemingly linked to pollinator management; *S. multiflora* will be the subject of a forthcoming paper (Lee *et al.*, in prep.). Another non-typical species is an as yet undescribed species from central Sarawak which has the spathe limb crumbling irregularly (Fig. 17).

The Multiflora Group is of particular interest in studies on adaptation to rheophytic habitats and on the phylogeny of the Schismatoglottideae since it shares vegetative architecture with the obligate rheophytic satellite genera *Aridarum* Ridl., *Bucephalandra* Schott, *Phymatarum* M. Hotta and *Piptospatha* N. E. Br., while sharing floral characteristics notably with *Piptospatha*, in which, unlike other satellite genera there exists two types of spathe senescence mechanics (see Bogner & Hay, 2000) and with *Phymatarum* in which there is combination of characters linking *Schismatoglottis* (urceolate persistent lower spathe) to the satellite genera *Aridarum* and *Bucephalandra* (horned thecae) and elongated micropylar appendage (all satellite genera).

The second author is currently working on the molecular phylogeny of the Multiflora Group and satellite genera in order to test monophyly of these taxa and to try to establish understanding of the evolutionary trends relating to floral characters and vegetative adaptations to rheophytism.

Calyptrata Group

Species closely allied to *S. calyptrata* (Fig. 18), e.g., *S. niahensis* A. Hay (Fig. 19), have the spathe limb caducous just prior to male anthesis, abscising cleanly at the top of the lower spathe and falling either in a single piece, or breaking into regular or

Fig. 19. *Schismatoglottis niahensis* A. Hay at the end of male anthesis.

Fig. 20. *Schismatoglottis wallichii* Hook. *f.* notable for the spathe limb shedding, splitting into regular pieces that adhere to one another and then contract acropetally before falling as a coherent unit.

Fig. 21. *Schismatoglottis motleyana* (Schott) Engl. is notable for the spathe shedding in a single piece as the adaxial epidermis sloughs away.

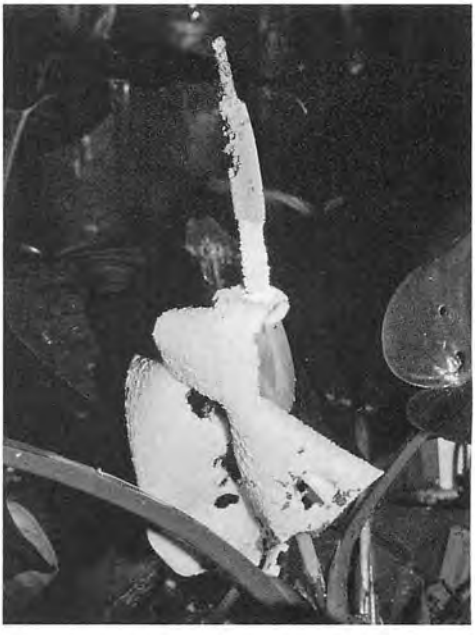

Fig. 22. *Schismatoglottis wongii* A. Hay from SE Sabah resembles *S. motleyana* (Schott) Engl. in its spathe mechanics.

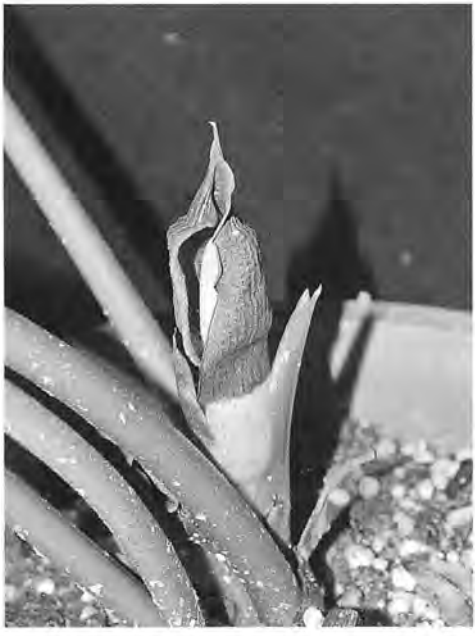

Fig. 23. *Schismatoglottis clarae* A. Hay is so far unique in the Calyptrata group by the spathe limb deliquescing to form a sticky paste that then dries onto the spadix before being shed.

Fig. 24. *Schismatoglottis longifolia* Ridl. is notable for the spathe limb barely opening and then persistent after anthesis before gradually degrading and falling while still clasping the spent parts of the spadix.

irregular pieces, while the tissue is still fresh, leaving the male zone and appendix (if present) exposed. However, there are several other senescence types occurring in the Calyptrata Group, which is otherwise defined by mostly hapaxanthic shoots, the petiolar sheath fully attached and usually long compared with the petiole length.

Schismatoglottis wallichii Hook. *f.* sheds the spathe limb by it splitting into regular pieces that adhere to one another and then contract acropetally so that the spathe limb is drawn up the spadix, rather in the manner of an Austrian blind, before falling in a loosely coherent unit (Fig. 20). *Schismatoglottis wallichii* is unusual in the Calyptrata Group by virtue of the spadix fertile to the tip (or very rarely with a few vestigial staminodes).

Schismatoglottis motleyana (Schott) Engl. (Fig. 21) and *S. wongii* A. Hay (Fig. 22) are notable for the spathe shedding in a single piece but not before the adaxial epidermis has begun to slough away in a series of rectangles and squares. *Schismatoglottis clarae* has a spathe limb that deliquesces to form a sticky paste that then dries onto the spadix before being shed when the spent portions of the spadix are shed (Fig. 23).

The widespread (one of only three *Schismatoglottis* species co-present in West Malaysia and Borneo) but never abundant *S. longifolia* has the spathe limb barely opening and then persistent after anthesis before gradually degrading and falling while still clasping the spent parts of the spadix (Figs. 24 & 25). The clustered, nodding inflorescences and infructescences are diagnostic for this species and an interesting link to the nodding inflorescences of *Piptospatha* N.E.Br.

Tecturata Group

At the time of publication of Hay & Yuzammi (2000) the Tecturata Group comprised just two species (*S. tecturata*

Fig. 25. *Schismatoglottis longifolia* Ridl. post anthesis with the spathe limb and spent parts of the spadix fallen. Note the nodding inflorescences and infructescences that are diagnostic for this species.

Fig. 26. *Schismatoglottis tecturata* (Schott) Engl. at late female anthesis.

(Schott) Engl. and *S. petri* A. Hay) allied by a vegetative architecture unique for the genus (foliage leaves alternating with prophylls or cataphylls) and the spathe with only the marginal and distal parts of the spathe limb withering after anthesis with the remainder persisting well into infructescence development (Figs. 26 & 27). Subsequently a further species, *S. jipomii* P. C. Boyce & S. Y. Wong has been described for the group (Boyce & Wong, 2007) which has the spathe limb caducous at the constriction and falling in a single or only a few pieces (Figs. 28 & 29). The senescence mechanics of *S. jipomii* thus approach species in the Multiflora Group (q.v.). Most interesting is that the vegetative appearance of the Multiflora and Tecturata Groups is overall very similar although derived from quite different architectural processes.

Additionally, a further three novelties belonging to the Tecturata Group (as yet unflowered but each vegetatively distinct) are awaiting description.

CONCLUSIONS

This very preliminary survey of the mechanics of spathe senescence reveals that the 'spathe deciduous' statement for *Schismatoglottis* is grossly oversimplified, as too is the view that movements of the spathe are associated with simply preventing self pollen from entering the lower spathe and coming into contact with the female flowers.

Based on fieldwork observations undertaken by us and our students (Lee *et al.*, in prep) it is clear that there is an intricate series of events involved linking the movement of the spathe, the phasing of the fertile events, the management of the pollinators and ultimately the development, successful maturation and dispersal of the fruits and seeds in *Schismatoglottis* and the other genera of the Schismatoglottideae.

Much needs to be done before we are in a position to attempt an overall presentation on the breadth of spathe/spadix and pollinator and dispersal interactions. Aside

Fig. 27. *Schismatoglottis tecturata* (Schott) Engl. at late male anthesis with the marginal and distal parts of the spathe limb withering.

Fig. 28. *Schismatoglottis jipomii* P. C. Boyce & S. Y. Wong differs from other described members of Tecturata group by the caducous spathe limb falling in a single or only a few pieces.

Fig. 29. *Schismatoglottis jipomii* after the spathe limbl was fallen.

from a greatly expanded study of *Schismatoglottis* it is vital that other genera of the Schismatoglottideae are sampled.

FURTHER RESEARCH

It is desirable that inflorescence developmental studies be undertaken in conjunction with greatly expanded field observations of spathe mechanics to determine if the abscission layer is homologous throughout the tribe and thus perhaps uniquely derived. Many more pollination and dispersal observations are required to link into forthcoming phylogenetic research.

As ever with non-woody mesophytic taxa the available herbarium materials and associated field data are woefully inadequate; anyone contemplating undertaking fieldwork in SE Asia is warmly encouraged to contact either author for advice on the collection, preparation and data recording of Araceae vouchers.

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