Rheophytism in Bornean Schismatoglottideae (Araceae)

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Abstract—The Schismatoglottid Alliance (tribes Schismatoglottideae, Cryptocoryneae and Philonotieae: Araceae) has been shown to be monophyletic in a previous study based on two cpDNA regions (matK and trnL-F). Here, ten additional taxa of Schismatoglottideae were sequenced, including two extra-Bornean Piptospatha species, and the type species of Hottarum, unavailable at the time of the previous analyses. Phylogenetic analyses were performed by using parsimony, likelihood (RAxML and likelihood ratchet PAUP*), and Bayesian inference to determine the placement of these additional taxa within Schismatoglottideae. The resulting tree topology supports, 1) a monophyletic West Sarawak clade comprising three genera: Aridarum, Bakoa, and Piptospatha; and 2) a supra-Lupar Line (the boundary between two of the known Bornean biochores) clade comprising the ‘Schismatoglottis’ josefi complex. Nineteen morphological, ecological, and geographical characters were coded and mapped using parsimony (unordered model) onto the Bayesian tree to investigate incidents of homoplasy or apomorphic status of morphologies presumed significant in the evolution of rheophytism. The morphologies proposed here as the primary mechanisms adaptive for rheophytism in Bornean Schismatoglottideae are: root/shoot disarticulation; a free ligular sheath; and marcescent senescence of the ligule. Two morphologies formerly used as generic definers, and previously treated as homologous: presence of a micropylar appendage, and thecae horns, are shown to be homoplastic.

Keywords—Araceae, Borneo, character mapping, phylogeny, rheophytic, Schismatoglottideae.

Borneo is an area with exceptionally high floristic endemism, often at highly localized levels (e.g. Raes et al. 2009; Wong 1998). The extreme heterogeological nature of the island, with limestones, sandstones, shale, and ultramafic substrates often intercalated with each other, have been put forward as one of the most likely reasons for the high endemism (Hutchison 1989). The topographical profile of Borneo, with extensive networks of rivers and streams producing a dissected landscape, the presence of a considerable altitudinal spectrum (Moss and Wilson 1998), and the processes by which Borneo accreted from Laurasia (Sundaland) during the season of low water level (van Steenis 1981, 1987). Rheophytes widespread in Borneo include, e.g. palms: Pinanga rivularis Becc. and P. tenella (H. Wendl.) Scheff.; shrubs: Myrmeconauclea strigosa (Korth.) Merr. (Rubiacaeae), and Osmoxylon borneense Seem. (Araliaceae); and trees: Antidesma neurocarpum var. linearifolium (Pax & K. Hoffm.) Petra Hoffm. (Euphorbiaceae), Fagraea stenophylla Becc. ex Merr. (Gentianaceae), Sandoricum borneense Miq. (Meliaaceae), and Syzigium tetragonocladium Merr. & L. M. Perry (Myrtaceae). Among Bornean-endemic rheophytic species of restricted distribution: Aglaia rivularis Merr. (Meliaaceae: east Sabah only), Antidesma stenophyllum Merr. (Euphorbiaceae; Sarawak), and Phyllanthus kinabalinicus Airy Shaw (Euphorbiaceae; Kinabalu in Sabah) are noteworthy and point to multiple times of derivation of rheophytism (Wong 1998).

Rheophytes are characterized by narrow leathery leaves and a firmly attached, usually epilithic stem. Borneo, particularly Sarawak and Brunei, for reasons not fully understood, appears to greatly favor rheophytism, with this ecological specialization derived multiple times in a range of flowering plant families and ferns (van Steenis 1981, 1987). Rheophytes widespread in Borneo include, e.g. palms: Pinanga rivularis Becc. and P. tenella (H. Wendl.) Scheff.; shrubs: Myrmeconauclea strigosa (Korth.) Merr. (Rubiacaeae), and Osmoxylon borneense Seem. (Araliaceae); and trees: Antidesma neurocarpum var. linearifolium (Pax & K. Hoffm.) Petra Hoffm. (Euphorbiaceae), Fagraea stenophylla Becc. ex Merr. (Gentianaceae), Sandoricum borneense Miq. (Meliaaceae), and Syzigium tetragonocladium Merr. & L. M. Perry (Myrtaceae). Among Bornean-endemic rheophytic species of restricted distribution: Aglaia rivularis Merr. (Meliaaceae: east Sabah only), Antidesma stenophyllum Merr. (Euphorbiaceae; Sarawak), and Phyllanthus kinabalinicus Airy Shaw (Euphorbiaceae; Kinabalu in Sabah) are noteworthy and point to multiple times of derivation of rheophytism (Wong 1998).

Studies on rheophytic plants to date have focused primarily on ferns (Imaichi and Kato 1997; Kato and Imaichi 1992), Lamiaceae (Pollard and Paton 2001), Asteraceae (Nomura et al. 2006; Mitsui et al. 2007; Tyukaya 2002; Tyukaya et al. 2006; Usukura et al. 1994), and Rubiaceae (Razafimandimbison et al. 2005; Sonké et al. 2007). In Araceae, although numerous papers have dealt with describing novel rheophytic taxa (e.g. Bogner 1983, 1984a, 1984b; Bogner and Hay 2000; Boyce 1994; Boyce and Wong 2006,
outside Borneo in the Philippines and Sulawesi (Hay and S. Y. Wong & P. C. Boyce obligate). A. okadae which over half of the so-far described species are obli-

ttotL-F, plus the 3’ portion of the trnK intron (trimmed to 19 bp). Ten taxa were newly sequenced: Aridarum caulescens [Ar2311], Aridarum nicolsonii [Ar480], Aridarum purseglovei [Ar3096], Hottarum truncatum [Ar3080], Ooia grabowskii [Ar2339], Piptospatha perakensis [Ar2603], Piptospatha ridleyi [Ar2602], Schismatoglottis macrocarpa [Ar607], Schottarum sarikeense [Ar1605], and Schottarum saricinata [Ar2394], and deposited into GenBank under Accession nos.: JN774852-JN774895 (Appendix 1). Outgroup sequences were obtained from GenBank, selected based on Cabrera et al. (2008) and Cusimano et al. (2011): Calla palustris L., Stylochaeton bogneri Mayo, Zamioculcas zamiifolia (Lodd.) Engl., and Gonatopus angustus N. E. Br. Voucher information and GenBank accession numbers are provided in Appendix 1. The combined data matrix has been deposited to TreeBASE (study number TB2-S12617).

DNA Extraction, PCR Amplification and Sequencing—DNA was extracted using the protocol and primers in Wong et al. (2010). PCR products were viewed again using a 1% agarose gel, and if a single clear band was present, the products were sent for sequencing in forward and reverse directions at First BASE Laboratories Sdn. Bhd., Selangor, Malaysia.

Sequence Alignment and Phylogenetic Analyses—Sequences obtained were manually trimmed, assembled for each species, checked by eye, and then edited. Sequences from different species were aligned and a contig was created using BioEdit ver. 5.0.6 (HALL 1999). New sequences were then aligned with the sequences from Wong et al. (2010). Gaps were treated as missing data. Phylogenetic analyses were performed with PAUP*4.0b10 (Swofford 2002) for maximum parsimony (MP) recon-

Character Mapping—Sixteen morphological characters were identified and scored. The geological and ecological niche where each taxon occurred, and its habit were recorded and scored as well. Table 1 shows the characters and their states. Characters for the ingroup taxa were recorded through field observations, and from plants in cultivation in the Botanical Research Centre, Semenggob, Kuching, Sarawak, since 2004. Characters for the outgroup taxa were based on Mayo et al. (1997) and Bogner (pers. comm.). Some of these characters (character 2,
Table 1. Morphological, ecological, and geological characters (and their states) used in this study.

<table>
<thead>
<tr>
<th>Character</th>
<th>State 1</th>
<th>State 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shoot/root disarticulation</td>
<td>presence</td>
<td>absence</td>
</tr>
<tr>
<td>Petiolar sheath attachment</td>
<td>fully attached</td>
<td>half way and above shortly auriculate</td>
</tr>
<tr>
<td>Pedicel sheath</td>
<td>caducous</td>
<td>marcescent</td>
</tr>
<tr>
<td>Pedicel posture</td>
<td>erect</td>
<td>spreading</td>
</tr>
<tr>
<td>Floret placement at anthesis</td>
<td>Inflating</td>
<td>not inflating</td>
</tr>
<tr>
<td>Spathe limb movement</td>
<td>spreading</td>
<td>pendent split</td>
</tr>
<tr>
<td>Spathe limb condition</td>
<td>caducous</td>
<td>persistent</td>
</tr>
<tr>
<td>Ecological niche</td>
<td>riverine</td>
<td>gallery</td>
</tr>
<tr>
<td>Geology</td>
<td>Multisubstrates</td>
<td>limestone</td>
</tr>
<tr>
<td>Micropylar appendage</td>
<td>presence</td>
<td>absence</td>
</tr>
<tr>
<td>Thecae horn</td>
<td>presence</td>
<td>absence</td>
</tr>
</tbody>
</table>

Results and Discussion

Matrix Characteristics—The combined plastid dataset was 2,099 bp in length, 1,586 for matK and 513 for trnL-F. In the combined analysis, 1,666 bp were constant, 251 bp variable but parsimony uninformative, and 182 bp (8.7%) parsimony informative.

Phylogenetic Analysis—Analysis from the matK region alone (tree not shown) strongly supported the Schismatoglottid Alliance proposed by Wong et al. (2010): Philonotieae + (Cryptocoryneae + Schismatoglottideae) (ML 100%, PP 1.00); Cryptocoryneae + Schismatoglottideae, (ML 91%, PP 0.98); Apoballis + the rest of Schismatoglottideae (ML 65%, PP 0.90). Next, H. truncatum [Ar3080] was supported as sister to the rest of Schismatoglottideae excluding Apoballis in the likelihood analysis (ML 88%). In contrast, trnL-F analyses provided poor support for separation of ingroups from the outgroup taxa (ML <50%).

The MP analysis generated 9,717 MPTs with a length of 633 steps, a consistency index (CI) of 0.76 (CI excluding uninformative characters = 0.58), and retention index (RI) of 0.77. Tree topology from the BI analysis was identical to the ratchet likelihood analysis. Calla formed a polytomy with the other outgroup taxa in MP and BI, but it was supported as sister clade to the Schismatoglottid Alliance in the likelihood analysis (ML 94%) (Fig. 1). This likelihood analysis for the placement of Calla was the same to the tree topologies of Cabrera et al. (2008) and Cusimano et al. (2011).

The Schismatoglottid Alliance (sensu Wong et al. 2010) was supported in MP, ML and BI analyses for the combined regions (matK and trnL-F) (Figs. 1, 2). In the ML analysis, there was weak support (ML 78%) to separate Schismatoglottis clausula [Ar1582] and Schottarum sarikeense [Ar1605] from the main clade. (Schismatoglottis jitiainae [Ar376 + Ar1039] + Schottariella mirifica [Ar1615] + Pichinia disticha [Ar1716] + Ooria grabowskii [Ar294], Piptospatha ridleyi [Ar2602], and (Schismatoglottis motleyana [Ar1970] + S. trifasciata) formed polytomes with the core Schismatoglottis and “small” genera clades. The core Schismatoglottis clade had weak support (posterior probability, PP 0.82) (with the exclusion of taxa in the ‘Schismatoglottis’ josefi complex (Low et al. in prep.)) but inclusion of A. purseglovii [Ar3096]. This topology was similar in both ML analyses: ratchet PAUP* and RAxML. However, in ML and BI analyses, a core Schismatoglottis + O. grabowskii [Ar294] clade showed weak support (PP 0.69).

Schismatoglottis tecturata [Ar466 + Ar2114] formed a strong relationship with ‘Schismatoglottis macrocardia’ [Ar607] (PP 0.96). In the ML analysis, a weak clade comprising the S. erecta complex with Schottarum sarikeense [Ar2394], S. tecturata [Ar466 + Ar2114], ‘S. macrocardia’ [Ar607], and S. asperata [Ar713.3] was formed. In the BI analysis, Schismatoglottis bauenis [Ar20], ‘S. evelynae’ [Ar1846], and S. converti [Ar2326] formed a weak clade (PP 0.89), but this was not supported in ML analysis.

The taxa formerly termed as the ‘satellite’ genera (Bogner and Hay 2000), were not supported as a monophyletic in

![Fig. 1. Maximum likelihood tree calculated with the combined plastid regions of trnL-F and matK, plus the 3’ portion of the trnK intron to show the placement of the Schismatoglottid Alliance (Schismatoglottideae, Cryptocoryneae, and Philonotieae) to the outgroups. Posterior probability values are indicated above branches and likelihood bootstrap values are indicated below branches. Scale bar indicates the expected number of substitutions per site.](image-url)
this study. However, there were two clades that include species from these “small” genera: A west Sarawak clade (ML 77%, PP 0.99) comprising *Aridarum nicolsonii* [Ar480 + Ar2098] + *Bakoa lucens* [Ar2097], *Piptospatha elongata* [Ar2052], *Aridarum borneense* [Ar2123] + *Piptospatha impolita* [Ar2141]; and a supra-Lupar Line (the Lupar Line marks the boundary of two of the major Sarawak biochores, the name derived from the Lupar River) clade comprising the ‘Schismatoglottis’
This clade may be related to a single or repeated chloroplast capture event(s) that may reflect the geographical grouping. *Schismatoglottis* josefii + *Phymatarum* formed polytomies with *Hestia longifolia* [Ar2286], *Schismatoglottis monoplera* [Ar1966 + Ar1994], and *Aridurum purseglovei* [Ar1036]. *Hottarum truncatum* [Ar3080] fell into the polytomies as well.

The ML tree also showed that *O. grabowskii* and *A. purseglovei* appeared in three and four separate positions respectively, with *A. purseglovei* [Ar3096] falling within the core *Schismatoglottis* clade. The phylogenetic relationships within the “small” genera remain unsatisfactory. However, preliminary results from ITS are better resolved (Low et al. 2011).

**Character Mapping Analyses—** Parsimony reconstruction of geology (character 19) was 37 steps; this was followed by inflorescence posture (character 7), lower spathe dispersal mechanics (character 14) and infructescence orientation (character 13), with 28, 27, and 25 steps respectively (Table 2). This was similar to the likelihood reconstruction of these characters with likelihood values ranging from $-\ln L = 134.539$–70.163. As CI serves to measure the relative amount of homoplasy, ecological niches (character 17) had the best fit on the tree, with CI = 0.292. The lower spathe dispersal mechanics (character 14, CI = 0.259), and lower spathe movement during anthesis (character 9, CI = 0.25) both have high values. Habit (character 18), received CI = 0.25. Retention index (RI) measures the proportion of synapomorphy expected from a data set that is retained as synapomorphic as the CI was exaggerated by autapomorphies. Seeds (character 15, RI = 0.818), and placenta (character 11, RI = 0.735), have high RI values. The inflorescence morphology and its behavior during anthesis also have high RI values, with post anthetic

<table>
<thead>
<tr>
<th>Character</th>
<th>Parsimonious steps $-\ln L$</th>
<th>Consistency index</th>
<th>Retention index</th>
</tr>
</thead>
<tbody>
<tr>
<td>Geology</td>
<td>37</td>
<td>134.539</td>
<td>0.162</td>
</tr>
<tr>
<td>Inflorescence posture</td>
<td>28</td>
<td>94.277</td>
<td>0.107</td>
</tr>
<tr>
<td>Lower spathe dispersal mechanics</td>
<td>27</td>
<td>112.043</td>
<td>0.259</td>
</tr>
<tr>
<td>Infructescence orientation</td>
<td>25</td>
<td>70.163</td>
<td>0.08</td>
</tr>
<tr>
<td>Ecological niches</td>
<td>24</td>
<td>113.451</td>
<td>0.292</td>
</tr>
<tr>
<td>Post anthetic lower spathe orifice</td>
<td>20</td>
<td>83.018</td>
<td>0.15</td>
</tr>
<tr>
<td>Habit</td>
<td>20</td>
<td>92.430</td>
<td>0.25</td>
</tr>
<tr>
<td>Leaf blade position</td>
<td>20</td>
<td>67.448</td>
<td>0.1</td>
</tr>
<tr>
<td>Spathe limb senescence</td>
<td>19</td>
<td>61.821</td>
<td>0.105</td>
</tr>
<tr>
<td>Shoot/root disarticulation</td>
<td>18</td>
<td>52.519</td>
<td>0.056</td>
</tr>
<tr>
<td>Lower/ spathe limb horizon</td>
<td>17</td>
<td>64.159</td>
<td>0.118</td>
</tr>
<tr>
<td>Petiolar sheath attachment</td>
<td>17</td>
<td>66.861</td>
<td>0.118</td>
</tr>
<tr>
<td>Thecae horn</td>
<td>13</td>
<td>38.774</td>
<td>0.077</td>
</tr>
<tr>
<td>Micropylar appendage</td>
<td>12</td>
<td>38.415</td>
<td>0.083</td>
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<tr>
<td>Posterior costa</td>
<td>11</td>
<td>35.318</td>
<td>0.091</td>
</tr>
<tr>
<td>Placenta</td>
<td>10</td>
<td>36.386</td>
<td>0.1</td>
</tr>
<tr>
<td>Ligule senescence</td>
<td>9</td>
<td>34.304</td>
<td>0.222</td>
</tr>
<tr>
<td>Lower spathe movement during anthesis</td>
<td>8</td>
<td>41.503</td>
<td>0.25</td>
</tr>
<tr>
<td>Seeds</td>
<td>7</td>
<td>31.251</td>
<td>0.143</td>
</tr>
</tbody>
</table>
sister to the rest of Schismatoglottideae, retains a fully-attached petiolar sheath, as do species of the Schismatoglottis Calyptrata Group, Corneri Group, Tecturata Group, and Hestia. Hestia is assumed to have retained the fully-attached petiolar sheath, although it has developed a unique suite of adaptations to fire-prone habitats; Hestia is the only genus sharing similar habitat (kerangas (tropical heath forest) formations, or on raised podsol in swampy areas) with Neotropical Philonotion (savanna forest on often inundated white sand) (Wong and Boyce 2010a).

The Asperata Group has a petiolar sheath that is provided with a distinct persistent terminal auricle, while a group of mostly novel species (Boyce et al. in press) centered on S. hottae Bogner & Nicolson has a greatly extended persistent ligule. Therefore free ligules (Fig. 4D) appear to be twice-derived in Schismatoglottideae: plesiomorphic in the “small” genera, and apomorphic for the Multiflora Group.

(Character 3) Ligule Senescence—The nature of the ligule senescence process in the Multiflora Group, and the “small” genera, is for the most part rapidly drying and thence marcescent. Ligules are mostly marcescent in the “small” genera. Notable exceptions are non-rheophytic Pichinia, and Schottariella, which are rheophytic in slow moving water. Both have persistent ligules. The free ligular portion of the leaf sheath protects innovations when fresh and senesces when that function is over. In the ‘Schismatoglottis’ josefii complex and Phymatarum, ligules are semi-persistent, and shoots do not disarticulate. These features may be functionally associated with these plants inhabiting muddy banks of slower moving rivers, rather than rocky banks of more violent rheophytic habitats. The above-mentioned clade occurs only in northeastern and central Sarawak. In Schismatoglottis, ligules could be marcescent, caducous, or persistent which again, points to multiple ligule origins.

(Character 4) Posterior Costae—Well-developed posterior costae are a prominent feature of most species of the Calyptrata Group (sensu Hay and Yuzammi 2000). Elsewhere in Schismatoglottis well-developed posterior costae occur in S. corneri A. Hay (Corneri Group sensu Hay and Yuzammi 2000) and in the S. asperata and S. multinervia M. Hotta groups sensu Boyce and Wong. No species belonging to the Multiflora Group, and none of the “small” genera display any posterior lobe development.

(Character 5) Leaf Blade Position—Leaf blade position relative to the petiole is a useful diagnostic character within the informal groups in Schismatoglottis. The leaf blade pendent relative to the petiole is the most common state in the Multiflora Group, where species are frequently associated with vertical growing surfaces such as river banks and waterfalls. Overall, the most common leaf blade posture is...
spreading, with the petiole erect to sub-erect and the blade set at more than 60° to the petiole (measured abaxially). The least common posture is blade erect, e.g. *S. lingua* A. Hay.

**Character 6** Lower/Spathe Limb Horizon—In its typical form, the spathe in Schismatoglottideae is differentiated into a lower persistent portion enclosing the female zone of the spadix and an ephemeral spathe limb subtending the male zone and appendix. The point of differentiation is usually marked by a constriction, less often parallel or rarely flaring.

**Character 7** Inflorescence Posture—The inflorescence position relative to the peduncle is taxonomically diagnostic. The inflorescences undergo flexing and movement of the peduncle either basally at the insertion on the plant or distally at the insertion of the inflorescence on the peduncle. Such movements are a function of positioning the infructescence into an optimal position for fruit/seed dispersal. The character states within *Schismatoglottis* are: inflorescence orthotropic relative to peduncle, with post floral inflorescences decline by peduncle flexing; this is the universal character morphology for the Calyptrata Group. Other groups in *Schismatoglottis* have an orthotropic inflorescence remaining orthotropic throughout fruiting (e.g. *S. asperata* and *S. barbata* complexes), inflorescence nodding, carried on erect peduncles, which either remain erect into fruiting (Corneri Group) or become declinate by basal flexing of the peduncle (*S. erecta* (Multiflora Group), and *H. longifolia*, and inflorescence is nodding with peduncle spreading to decline (Multiflora Group, but this is not universal). Rheophytic species of the Multiflora Group the inflorescence faces down with the opening of the spathe positioned ventrally and thus sheltered from water flow. The mechanics of inflorescence maturation, posture, pollination and dispersal are intimately linked.

**Character 8** Spathe Limb Senescence—The often cited ‘spathe limb deciduous’ for *Schismatoglottis* is a simplification. The Calyptrata Group has the spathe limb caducous that is absicssing and falling while still yet to degrade. Although even here the spathe limb often begins to fragment into regular and irregular fragments which remain fresh. Observation of several species, purportedly (related to each other in the *S. motleyana*/*S. wallichii* Hook. f. complexes) shows a consistent series of spathe limb movement associated with abscission. In the Multiflora Group, spathe limb shedding is also caducous, but again whether the spathe limb is shed in one piece (e.g. *S. maei* P. C. Boyce & S. Y. Wong, *S. multiflora, S. nicolsonii*, etc.) or fragments into regular or irregular pieces (e.g. *Schismatoglottis josefii complex*) is taxonomically and probably phylogenetically significant. *Phymatarum* parallels the Calyptrata Group of *Schismatoglottis* in that the spathe limb is caducous. *Ariderum* and *Bucephalandra* are mainly caducous, although *Ariderum* often has the spathe at least partially marcescent. The spathe limb of *B. lucens* is fully persistent late into fruiting and thence rapidly marcescent and is intimately linked to dispersal (see Boyce and Wong 2008).

**Character 9** Lower Spathe Movement During Anthesis—Almost all the species investigated in the Schismatoglottideae undergo a spathe loosening and inflation process early in anthesis. Within the “small” genera, the tightly furled inflorescence buds of *Piptospatha* and *Bucephalandra* are notable for their marked and rapid inflation during anthesis, when the lower spathe swiftly becomes saliiform through the flaring of the lower spathe at the onset of female anthesis. *Ariderum* shows similar but somewhat less marked flaring; *Ariderum* inflorescences tend to open more slowly than those of *Piptospatha*. *Bakoa lucens*, in many respects, parallels the limb mechanics of *Apoballs* with the lower spathe loosening and then clasping again, and the spathe limb scarcely opening. Similar spathe mechanics are observed in *S. corneri*, and *Hestia*. *Phymatarum* resembles the Calyptrata Group in *Schismatoglottis* in its spathe limb movement which is inflating. All groups apart from the Asperata Group (flaring) in *Schismatoglottis* possess inflating inflorescence during anthesis.

**Character 10** Post Anthetic Lower Spathe Orifice—Spathe morphology during fruit maturation varies considerably between taxa of Schismatoglottideae. Within *Schismatoglottis*, by far the most common morphology is an urceolate lower spathe with a constricted orifice; the constriction corresponding to the lower spathe constriction that demarcates the junction between the lower spathe and the spathe limb just prior to and at anthesis. The post-anthesis lower spathe of *Phymatarum* is very similar. Within *Schismatoglottis*, exceptions to this generalized lower spathe are those with the orifice widely open, but not flaring. This morphology occurs in several species complexes in Hay & Yuzammi’s Asperata Group, most notably the *S. asperata* Group. In the “small” genera, with the exception of *Phymatarum* and *Ooia*, all lower spathe, where they persist into fruiting (as opposed to the spathe remaining completely persistent), are widely flaring and are referred to as splash cups. Splash cups and their concomitant dispersal mechanisms are multiply derived in the “small” genera.

**Character 11** Placentation—Parietal placentation is apomorphic for *Schismatoglottis* while basal placentation is plesiomorphic for the “small” genera. Placentation in *Schismatoglottis* is described as having two to three parietal placentae with numerous ovules (Hay and Yuzammi 2000; Bogner and Hay 2000). However, these data are based on few actual observations beyond those made on the most common species found in tropical Asia: *S. calyptrata*. Hotta observed that one species of the Multiflora Group, *S. monoploca* M. Hotta has only one placentum (Hotta 1966).

The amount of space available on a basal placenta limits the number of ovules that may be accommodated, and therefore basal placentation is usually associated with few seeded fruits. By compensation, seeds tend to be larger than is the case with parietal placentation. The larger seeds may be advantageous in rheophytic habitats; the additional mass of the individual seeds enabling them to better survive dispersal in spate rivers; furthermore it is conjectured that the larger seeds are better suited to the production of micropylar appendages.

*Bakoa lucens* has seeds arranged on an annulate basal placenta. The remainder of the “small” genera have an umbonate basal placenta. Among the “small” genera, *Phymatarum* is the one exception in having parietal placentae and numerous seeds. Cryptocoryneae possesses a loculicidal apocarp, while Philonotieae has a single parietal placenta with 1–4 seeds.

**Character 12** Thecae Horns—Thecae horns (Fig. 41) occur only in the “small” genera, and in a somewhat different morphology to their occurrence in Cryptocoryneae. Diversity of thecae horn structure, pollen release, and pollen presentation, have now been more closely observed and
morphological mapping onto a phylogenetic tree suggests that theca horns are independently derived at least four times in the Schismatoglottideae (Low et al. in prep.). Derivations occur in the Aridarum/Bucephalandra clade; once in Phymatarum, once in Schottariella, and once in the Aridarum sect. Caulaesentia M. Hotta. The last is presently an unresolved polytomy that does not cluster with Aridarum s. s. Theca horns in Aridarum arise from excavated block-like stamens in which the individual thecae are not clearly differentiated from one another, and the horns have thick bases and strongly tapering tips. In Aridarum, theca horns are positioned laterally, either two on one side of the theca directed into the theca excavation, or one ventral and one dorsal with the end of the theca excavation (Bogner and Hay 2000). Theca horns in Bucephalandra and Phymatarum are uniformly slender needle-like structures arising from differentiatied globose to ellipsoid thecae. In Schottariella, theca horns become visible only at the onset of staminate anthesis when one horn ‘unfolds’ from a groove in the top of each theca. Thecae horns of Cryptocoryneae (Cryptocoryne and Lagenandra) are short and cylindrical.

(Character 13) Infructescence Orientation—This character is closely correlated to lower spathe dispersal mechanics (character 14). Splash cup (Fig. 4E) dispersal is here considered a crucial morphological adaptation to the rheophytic habitat in Schismatoglottideae. In all genera with splash cups studied to date the lower spathe persists, thickens, and becomes photosynthetic post-anthesis. Despite this seemingly common morphological derivation, evidence is that splash cups are derived multiple times in Schismatoglottideae. An erect splash cup occurs in Aridarum, Bucephalandra, and Piptospatha. Schottariella differs in producing a markedly oblique lower spathe orifice, and in the declinate peduncle. Ooia has evolved into a completely different mechanism with the entire spathe persistent late into fruit development and the peduncle declinate such that the persistent spathe tips touches, or is slightly submerged, in water. When the fruits are approaching ripeness, the extreme top margin and associated rostrum of the spathe are shed, enlarging the spathe orifice to allow spent flowers to be shed from the persistent spadix, and later to enable the mature fruits, which decompose at full ripeness, to be washed from the spathe via water turbulence (Wong and Boyce 2010b).

In post pollination Bakoia the persistent spathe turns green and thickens slightly while the peduncle becomes declinate, holding the spathe with the free margins downwards. At the onset of fruit maturity the peduncle twists through 180° and once more becomes semi-erect, to bring the spathe free margins to a dorsal position (relative to the peduncle) after which the spathe dries and turns brown swiftly. By reflexing of the two thirds adnate spadix, the spathe recovers and opens, tearing at the peduncle insertion to expose the fruits while at the same time the spathe limb remains distally convolute and clasps the remains of the spadix appendix (Boyce and Wong 2008).

(Character 14) Lower Spathe Dispersal Mechanics—Almost all species of Schismatoglottis regardless of whether the orifice constriction is tight or loose, release their fruit by longitudinal acrosopic splitting, with the separated portions of the lower spathe reflexing irregularly, or in partially-adherent blocks. Those species with a large proportion of the female zone adnate to the spathe undergo flexing of the spadix axis such that the interior surface of the lower spathe reflexes, presumably to better-present the ripe fruit. Fruit falls readily from the spadix axis. A notable exception to this lower spathe opening is S. tecturata, where almost the entire persistent lower spathe analogue is persistent, abscises basally and then splits longitudinally then basiscopically to reveal the fruits. This is an analog to the fruit-display mechanics that occurs in Homalomena.

The spathe of Ooia grabowskii is persistent late into fruit development at which point the extreme top margin and associated rostrum are shed by rapid marcescence, enlarging the spathe orifice to allow spent flowers to be shed from the persistent spadix. The mature fruits, which decompose at full ripeness, are washed from the spathe via water turbulence. Infructescences of Ooia are pendent, often with enlarged opening submerged in water (Wong and Boyce 2010b).

The splash cup is erect is almost all of the “small” genera. In Phymatarum, the lower spathe is urceolate with a narrow orifice as in most Schismatoglottis. It splits and the fruits are dispersed in the same manner as in Schismatoglottis.

(Character 15) Seeds—As noted above, all the “small” genera except Phymatarum are few-seeded with basal placenta.

(Character 16) Micropylar Appendage—Micropylar appendages, seed adaptations to anchoring, are present as variously elaborated structures in Aridarum, Bucephalandra, Piptospatha, Ooia, Phymatarum, and as a blunt rostrum in Bakoia, and Schottariella (Boyce and Wong 2008). Micropylar appendage morphology is not uniform. Observations of their functionally suggest that while all act as anchors, they function in different manners (pers. obs.). Phymatarum borneense, a plant occurring colonially on level banks of slow-moving rivers, has a micropylar appendage which is distally hooked, and seems to function as a grapnel to snag on moss or amongst roots (Fig. 4F). By comparison, Aridarum borneense has a pronounced micropylar appendage that does not function as a hook beyond the earliest stage of seed anchorage. Instead it splits into a fibrous web which appears to function much in the same way as the byssus in mussels. Interestingly, A. borneense occurs habitually on almost vertical rocky waterfalls, or on the leeward side of large boulders, in habitats offering little in the way of places to snag a hooked seed for long enough to enable germination to proceed securely (Ooi et al. in prep.).

(Character 17) Ecological Niches—Schismatoglottis has diversified into most ecological niches in Sarawak with the exception of Kerapah (the wet facies of kerangas). There are no true climbing species, although several have erect elongated stems that root along their lengths; obligate epiphytes are absent. Generally speaking, Schismatoglottis species which are colony-forming (e.g. the Calyptrata Group), favor flat to undulating terrain. Only rarely are species of the Calyptrata Group found on strongly inclined and rocky surfaces. Clustering and solitary species, typically the Asperata Group sensu Hay & Yuzammi, favor sloping to vertical surfaces typical of gallery forests, and rocky outcrops and steep earth banks, under high canopy, Chasmophytes in Schismatoglottis are uncommon and are thought to be adaptive. Species notable as obligate chasmophytes include the limestone associated taxa S. monoplacenta and S. baunensis (Multiflora Group) and S. ‘shaleicola’ (Asperata Group) among others. In the Tecturata Group, S. ‘evelynae’ is often chasmophytic (and there with a much elongated ‘climbing’ stem, but not obligately so. In many respects, chasmophytes
face some of the same ecological stresses as rheophytes, especially with regard to moisture availability during prolonged periods of dry weather.

(CHARACTER 18) HABIT—Rheophytes are flood-resistant plants, usually of tropical humid to wet forests, growing in or along swift-running streams or rivers up to the flood level. They are characterized by narrow leathery leaves and a firmly attached, usually epilithic stem. In addition to Schismatoglottideae, in which the majority of genera have some or all species with this habit, rheophytes are also found in *Homalomena*, *Anubias* Schott (equatorial west Africa), *New Guinea Holochlamys*, and rarely *Anthurium* (Neotropics).

In *Schismatoglottis* groups where species are predominately terrestrial mesophytes species occasionally occur adapted to rheophytism (e.g. *S. jelandii* P. C. Boyce & S. Y. Wong in the otherwise mesophytic terrestrial Asperata Group, and *S. ahmadii* A. Hay in the Calyptrata Group). In these examples there is suggestion of adaptive radiation into a new habitat. Equally, in groups where rheophytism is dominant but occasionally non-rheophytes occur, polarity appears to be rheophytic to non-rheophytic. However, in the *Schismatoglottis* Multiflora Group, there is a mosaic of mesophytic, obligate rheophytic, and facultative rheophytic taxa such that without an independent analysis using genetic data, it is impossible to attribute a plesiomorphic habitat preference.

Lithophytism (sometimes associated with chasmophytism, growing on vertical rocks under seasonally dry but perhumid, or continually wet conditions) is common in the frequently humid and provide an ideal habitat for both associated with water action. Therefore shale forests are to be located in isolated patches and they also tend to be degrades to form rich soil. Exposed shales in forests tend to reveal a wealth of geologically endemic taxa. Granite forest species can be regarded as classic mesophytes, with the forest usually heavily shaded and perhumid. What is interesting is that while prevailing conditions in gallery forests in any one area tend to be uniform, the aroid species favouring that habitat can be highly localized. A good example of locality dependence within a uniform habitat are *S. jittiniae* S. Y. Wong, *S. bellii*, *S. fugax*, and *S. cruelis* which are found in tiny highly localized discrete colonies in extensive tracts of apparently ecologically uniform forest.

Riverine deposited mudbanks and sandbanks are potentially one of the most difficult habitats for perennial plants to colonize. However, Araceae species are often well-adapted to this type of environment. In Schismatoglottideae, few species have made this their primary habitat, although *S. triviata* Hallier f., *S. consensua* and *P. borneense* are wholly confined to this environment.

**Generic Boundaries within Schismatoglottideae**—The phylogeny presented in this study does not support the generic boundaries of the “small” genera proposed by Bogner and Hay (2000). Furthermore, it failed to resolve the internal topology of *Aridarum*, *Bucephalandra*, and *Piptospatha*, and yet these genera individually display strong morphological patterns. Further studies are necessary before making changes to their circumscriptions.

One outcome of the current study has been to show that key morphological characters hitherto used to define genera have evolved through paraphyletic taxa (parallelism), polyphyletic taxa (convergent), or reversal, and that their use...
to define morphological-based phylogenies is misleading. Micropylar appendage (character 16) and thecae horn morphologies (character 12) are traditionally regarded as synapomorphic for the “small” genera. Treating these morphologies as a single origin is not in agreement with the phylogeny produced here. The convergent origins of these two morphological characters, singly or multiple times, has created an adaptive key to best fit an ecological lock.

**Radiation of Schismatoglottidaceae on Borneo**—Localized specific adaptations, in combination with restricted gene-flow and seed dispersal limitations, could well explain the remarkable level of species diversity in Schismatoglottidaceae seen today in Borneo. Where studies exist, Schismatoglottidaceae display poor dispersal rates for rheophytes (Ooi et al. in prep.), and taxa are not infrequently limited to a single stream, and “replaced” by different taxa in an adjacent stream. Therefore, the intervening non-riverine land (in Borneo often a series of ridges and non riverine valleys) between each stream function as an effective dispersal barrier, while independent river systems function as speciation-favoring “islands.” In a separate tribe, work on obligately rheophytic *Furtadoa sumatrensis* M. Hotta (Araceae: Homalomenaceae), reveals that pollen flow is restricted within a single river system, with any one particular river system harboring a genetically isolated population to that in the next (Mori and Okada 2001).

The sole obligate rheophytic aroid genus present in West Malaysia (*Piptospatha*), has not radiated into numerous localized species despite the relative abundance of isolated limestones and even occasional exotic geologies (e.g. the quartz of the Klang Gates near to Kuala Lumpur, and the massive schists of Gunung (Mt) Stong (Kelantan), etc.). Furthermore there are no rheophytic (obligate or otherwise) *Schismatoglottis* in the Peninsula, and within *Homalomena* few are rheophytes and none restricted to that ecology. It is possible that a combination of factors favor rheophytism on Borneo are in part or entirely absent in Peninsular Malaysia.

Species of *Schismatoglottis* are mostly adapted to mesophytic habitats. However, the genus contains a scattering of chasmophytic, and lithophytic niche-endemics. Rheophytism in *Schismatoglottis* is secondarily derived. The Multiflora Group, which is restricted to Borneo, has adapted to rheophytism on vertical (primarily rock) surfaces. Elsewhere in *Schismatoglottis* there are scattered species with obligate or facultative rheophytic ability in the Calyptrata Group (*S. alnadii*, obligate), Asperata Group (*S. jelandii*, facultative; various novel species, all obligate), and Tecturata Group (*S. jipomii* P. C. Boyce & S. Y. Wong & S. *pudenda* A. Hay, both facultative), but none display the extensive radiation and diversification present in the “small” genera.

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**Literature Cited**


Nanga Gaat, Kapit, Sarawak, 01.42 N, 113.26 E, P. C. Boyce & K. Jeland Ar134 (SAR), GQ221013, GQ220948; Schismatoglottis sp., Multiflora Group, Sg. Pat, Nanga Gaat, Kapit, Sarawak, 01.38 N, 113.24 E, P. C. Boyce & K. Jeland Ar108 (SAR), GQ221010, GQ220945; Schismatoglottis sp., Multiflora Group, Sg. Pat, Nanga Gaat, Kapit, Sarawak, 01.38 N, 113.24 E, P. C. Boyce & K. Jeland Ar114 (SAR), GQ221016, GQ220951; Schismatoglottis tecturata (Schott) Engl., Tecturata Group, Kubah National Park, Matang, Kuching, Sarawak, 01.36 N, 110.12 E, P. C. Boyce et al. Ar2114 (SAR), GQ221015, GQ220950; Schismatoglottis trifasciata Engl., Calyptrata Group,–, Chase 10692 (K), AM93332, AM920604; Schismatoglottis viridissima A. Hay, Calyptrata Group, Waterfall No. 1, Gunung Gading, Lundu, Kuching, Sarawak, 01.41 N, 109.51 E, P. C. Boyce & S. Y. Wong Ar2048 (SAR), GQ221017, GQ220952; Schottarum sarikeense P. C. Boyce & S. Y. Wong, Schottarum, Sg. Matob, Maradong, Sarakei, Sarawak, 01.52 N, 111.55 E, P. C. Boyce et al. Ar1615 (SAR), GQ221009, GQ220912; Stylochaeton bogneri Mayo, Outgroup,–, Chase 10685 (K), AM933327, AM920598; Zamioculcas zamiifolia (Lodd.) Engl., Outgroup,–, Chase 10686 (K), AM905778, AM920600.