

## 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 josefii* 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) and fragments of Gondwana (east coast of Sabah) have been postulated as causative as well (Meijaard 2004). In all probability, the extraordinary floristic endemism of the island is a result of all of these factors, and others besides, not the least of which is the high rainfall (three m annually) that most of the island receives for much of the year (Slik et al. 2009). For example, in each of Dipterocarpaceae, Ericaceae, Myristicaceae, Fagaceae, and Nepenthaceae, more than 50% of the species are endemic to Borneo. Of the plant families revised for the Flora Malesiana project, Borneo has the second highest occurrence of endemic species (37%) among the Malesian islands, after New Guinea (van Welzen and Slik 2009).

On Borneo, Araceae comprises ca. 400 described species in 39 genera (Boyce et al. 2010). Aside from high levels of island endemism (ca. 80% of species are restricted to Borneo) the aroids also show a remarkable level of highly localized endemism, often specific to a particular substrate. Bornean aroids are particularly abundant and diverse below 1,200 m (in contrast to much of the Neotropics, see Croat 1990, 1992). Aroids are enormously important as indicators of forest quality since they are both adaptive to localized ecological heterogeneity, and adversely influenced by forest disturbance (pers. obs. & P. C. Boyce, pers. comm.). Lifeforms of Araceae on Borneo comprise mesophytes, lithophytes, chasmophytes, rheophytes, and secondary hemiepiphytes. In contrast to the Neotropics, obligate epiphytes are almost wholly absent, represented by fewer than 15 species (Boyce et al. 2010).

The term ‘rheophytes’ was first coined by van Steenis (1981) although recognition of a distinct ecological concept was first noted by Ridley (1893), who termed it ‘stenophylly’, in his account of the flora of the Tembeling and Tahan rivers in then Malaya (Ridley 1893). Later, Beccari (1902, 1904) grouped plants of this habitat as ‘stenophyllous’ plants. The rheophytic habitat is defined as the region between the lowest and the highest water levels, where plant species are repeatedly buffeted and saturated by regular flash floods after heavy rainfall followed by exposure to dry conditions during the season of low water level (van Steenis 1981, 1987).

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: *Myrmeconuclea strigosa* (Korth.) Merr. (Rubiaceae), 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. (Meliaceae), and *Syzigium tetragonocladum* Merr. & L. M. Perry (Myrtaceae). Among Bornean-endemic rheophytic species of restricted distribution: *Aglaiia rivularis* Merr. (Meliaceae: east Sabah only), *Antidesma stenophyllum* Merr. (Euphorbiaceae; Sarawak), and *Phyllanthus kinabaluicus* 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,

2008; Hay and Yuzammi 2000; Okada and Mori 2000; Wong 2010), this is the first attempt to study the adaptive significance of their morphologies, and to understand these adaptations in a phylogenetic context.

Within Araceae, rheophytes are pre-eminent in tribe Schismatoglottideae, one of the three tribes (together with Cryptocoryneae and Philonotieae) of the Schismatoglottid Alliance (Wong et al. 2010). Bunting (1960) and other specialist Neotropical aroid collectors (notably Croat, sub exsiccatae) have repeatedly recorded that *Philonotion* Schott occurs along stream banks in forests bordering savannas or at least, if occurring in open sandy soil, there is always the presence of abundant moisture at the roots. However, *Philonotion* species have no clear morphological adaptations to rheophytism (stenophylly, disarticulation of vegetative units, dispersal mechanisms favoring water, etc.). Rheophytes also occur in Asian *Homalomena* Schott (Homalomenaceae), and *Rhaphidophora* Schott (Monstereae), West African *Anubias* Schott (Anubadieae), and the New Guinea endemic *Holochlamys* Engl. (Spathiphyllaceae), and rarely in Neotropical *Anthurium* Schott (Mayo et al. 1997; Croat et al. 2007). Why one tribe of Araceae, the Schismatoglottideae, should almost totally dominate rheophytic niches throughout Borneo and furthermore account for much of the rheophytism in the family, remains unclear.

Tribe Schismatoglottideae, is one of the most species-rich and diverse aroid taxa on Borneo, with more than 250 species, of which over 95% are endemic on the island. Besides the largest genus, *Schismatoglottis* Zoll. & Moritz, the tribe includes ten further genera each composed of one to a few species (hereafter referred to as "small" genera): *Apoballis* Schott, *Aridarum* Ridl., *Bakoa* P. C. Boyce & S. Y. Wong, *Bucephalandra* Schott, *Hestia* S. Y. Wong & P. C. Boyce, *Phymatarum* M. Hotta, *Pichinia* S. Y. Wong & P. C. Boyce, *Ooia* S. Y. Wong & P. C. Boyce, *Piptospatha* N. E. Br., and *Schottariella* P. C. Boyce & S. Y. Wong (Bogner and Hay 2000; Boyce and Wong 2008, 2009; Okada 2006; Wong and Boyce 2010a, 2010b, 2010c). With possible exception of *Apoballis*, all occur on Borneo. All except *Hestia*, *Piptospatha*, and *Schismatoglottis* are restricted to Borneo. All genera except *Hestia* and *Pichinia* contain rheophytic species; all genera except *Apoballis*, *Hestia*, *Pichinia*, and *Schismatoglottis* are entirely rheophytic.

*Schismatoglottis* on Borneo display rheophytism in species of the Calyptrata (few), Asperata (few), and Tecturata (some, none obligate) groups, while this ecology is dominant in the exclusively Bornean Multiflora Group (Bogner and Hay 2000; Boyce 1994; Boyce and Wong 2006, 2007, 2008, 2009; Hay 1996; Hay and Yuzammi 2000; Hotta 1965, 1966, 1976; Wong 2010; Wong and Boyce 2007) in which over half of the so-far described species are obligate rheophytes. In the *Schismatoglottis* Calyptrata Group, three species (*S. eymae* A. Hay, *S. luzonensis* Engl., and *S. subundulata* (Zoll. ex Schott) Nicolson) occur rheophytically outside Borneo in the Philippines and Sulawesi (Hay and Yuzammi 2000). *Apoballis* species occasionally occur as semi-rheophytes (with Sumateran *A. okadae* (M. Hotta) S. Y. Wong & P. C. Boyce obligate).

Wong et al. (2010) resolved the phylogenetic relationships of the Schismatoglottid Alliance at the tribal level, but various aspects of internal resolution remained unresolved. The first part of this new study includes *matK* and *trnL-F* data for an additional ten unsampled critical taxa of

Schismatoglottideae: two extra-Bornean *Piptospatha* species (*P. perakensis* (Engl.) Ridl. & *P. ridleyi* N. E. Br. ex Hook. f.), and the type species of *Hottarum*: *H. truncatum* M. Hotta. *Hottarum* is currently treated as congeneric with *Piptospatha* (Bogner and Hay 2000). In the second part, 19 morphological, ecological, and geological characters were coded and mapped onto the Bayesian tree to investigate the apomorphy and homoplasy of rheophytic-adaptive morphologies, and to infer the process of radiation of rheophytism in Schismatoglottideae on Borneo.

## MATERIALS AND METHODS

**Materials**—A total of 73 taxa of Schismatoglottideae, three taxa of Cryptocoryneae, and one taxon of Philonotieae were analysed for *trnL-F* and *matK*, 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 macrocardia*' [Ar607], *Schottarium sarikeense* [Ar1605], and *Schottarium sarikeense* [Ar2394], and deposited into GenBank under Accession nos.: JN177482-JN177489; JN177490-JN177499 (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 on a 1% agarose gel and purified using a Fermentas (Burlington, Ontario, Canada) PCR purification kit. Purified 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) reconstruction. All characters were equally weighted. The most parsimonious trees were obtained with heuristic searches of 1,000 replicates with random stepwise addition, tree bisection-reconnection (TBR) branch swapping, collapse of zero-length branches, with multiple tree option in effect, and saving 10,000 trees from each random sequence addition.

The most suitable nucleotide substitution model for each of the gene regions were selected in jModeltest ver. 0.1.1 (Posada 2008) using Akaike information criterion (AIC). The general time reversible (GTR + I + G) was the nucleotide substitution model selected. Maximum likelihood (ML) analyses were carried out by RAxML through the CIPRES portal (Stamatakis et al. 2008) for 10,000 replicates, and repeated 10 times to generate 100,000 replicates. The ML analysis was also repeated using the likelihood ratchet method through PAUP\* (Morrison 2007). The ML bootstrap values were estimated with 1,000 replicates using the same software. Bayesian inference (BI) phylogenetic analyses were performed with MrBayes ver. 3.1.2 (Huelsenbeck and Ronquist 2001). Markov Chain Monte Carlo (MCMC) was repeated twice to assure parameter convergence. The MCMC algorithm was run for 2,000,000 generations with one cold and three heated chains, starting from random trees and sampling one out of every 100 generations. The first 2,500 trees were discarded as burn-in. Remaining trees were used to construct 50% majority-rule consensus trees.

**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, Semenggoh, 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.

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1. Shoot/root disarticulation: presence <0>, absence <1>. 2. Petiolar sheath attachment: Fully attached <0>, attached only at base remainder ligulate <1>, attached half way and above shortly auriculate <2>. 3. Ligule senescence: caducous <0>, marcescent <1>, persistent <2>. 4. Posterior costae: presence <0>, absence <1>. 5. Leaf blade position: Pendent relative to petiole <0>, Spreading relative to petiole <1>, Erect <2>. 6. Lower/spathe limb horizon: constricted <0>, parallel <1>, flaring <2>. 7. Inflorescence posture: erect <0>, spreading <1>, nodding <2>, pendent <3>. 8. Spathe limb senescence: Caducous <0>, marcescent <1>, persistent <2>. 9. Lower spathe movement during anthesis: Inflating <0>, not inflating <1>, flaring <2>. 10. Post anthetic lower spathe orifice: constricted <0>, parallel <1>, flaring <2>, oblique flaring <3>. 11. Placentation: Basal <0>, parietal <1>. 12. Thecae horn: Presence <0>, absence <1>. 13. Infructescence orientation: pendent <0>, nodding, <1>, erect <2>. 14. Lower spathe dispersal mechanics: erect splash cup <0>, pendent splash cup <1>, pendent split <2>, pendent vortex <3>, lucens-type <4>, erect basicopic abscissing <5>, erect acrosopic abscissing <6>, dehiscent <7>. 15. Seeds: many <0>, very few <1>. 16. Micropylar appendage: Presence <0>, absence <1>. 17. Ecological niches: Undulating topography <0>, riverine <1>, gallery <2>, mudbanks <3>, sandbanks <4>, emergent limestone stacks <5>, forest swamp <6>, tropical forest heath <7>. 18. Habit: Terrestrial <0>, lithophytic <1>, rheophytic <2>, aquatic <3>, helophytic <4>, geophytic <5>. 19. Geology: Multisubstrates <0>, limestone <1>, sandstone <2>, shales <3>, granite <4>, white sand <5>, acidic peat <6>.

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6, 10, 12, 13 and 16, Table 1) have been regarded as apomorphies for the “small” genera (Hay and Yuzammi 2000; Bogner and Hay 2000). Character matrices were comprised of categorical data; four characters were binary and 15 multistate. Missing information was coded as ? and all characters were non-ambiguous. Character matrices were analysed in Mesquite ver. 2.74 (Maddison and Maddison 2010) using parsimony (unordered model) and likelihood under the Markov k-state one-parameter model (MK1), where all changes are equally probable. Matrices were mapped onto the 50% majority consensus rule trees from Bayesian analysis based on the combined *matK* and *trnL-F* regions. The purpose was to assess the character ‘fitness’ onto the tree, and to identify plesiomorphies, synapomorphies or homoplasies congruent to rheophytic habitat.

## 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 jitiniae* [Ar376 + Ar1039] + *Schottariella mirifica* [Ar1615]) + *Pichinia disticha* [Ar1716] + *Ooia grabowskii* [Ar294], *Piptospatha ridleyi* [Ar2602], and (*Schismatoglottis motleyana* [Ar1970] + *S. trifasciata*) formed polytomies 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 josefii* complex (Low et al. in prep.)] but inclusion of *A. purseglovei* [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 tectorata* [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. tectorata* [Ar466 + Ar2114], ‘*S. macrocardia*’ [Ar607], and *S. asperata* [Ar71.3] was formed. In the BI analysis, *Schismatoglottis bauensis* [Ar20], ‘*S. evelynae*’ [Ar1846], and *S. corneri* [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

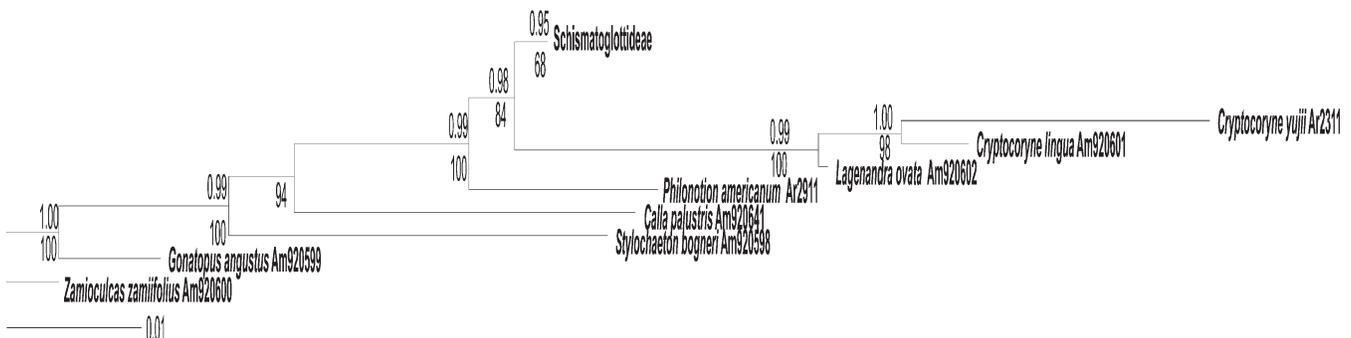


FIG. 1. Maximum likelihood tree calculated with the combined plastid regions of *trnL-F* and *matK*, plus the 3' portion of the *trnK* intron to show the placement of the Schismatoglottid Alliance (Schismatoglottideae, Cryptocoryneae, and Philonotieae) to the outgroups. Posterior probability values are indicated above branches and likelihood bootstrap values are indicated below branches. Scale bar indicates the expected number of substitutions per site.

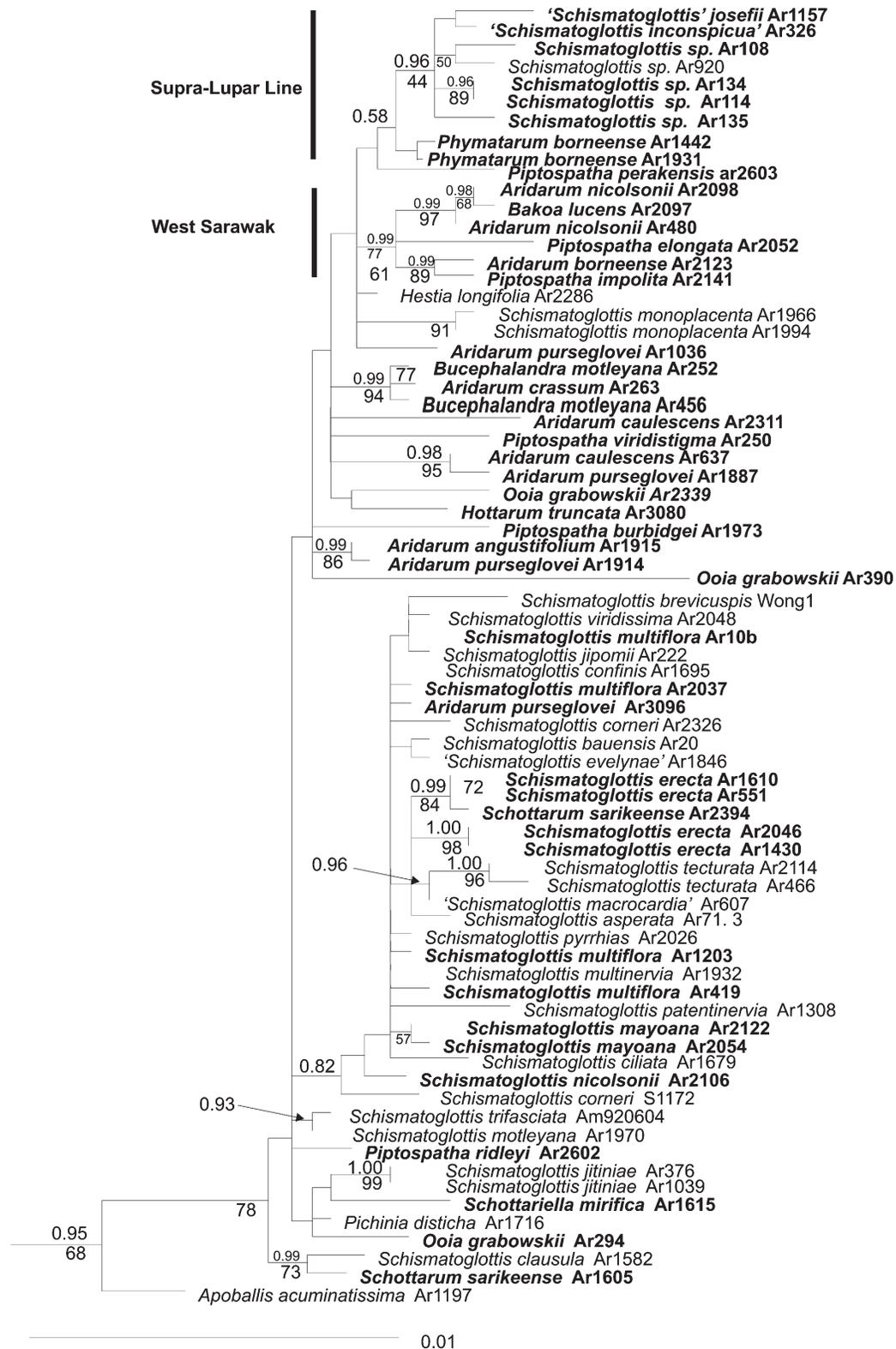


FIG. 2. Maximum likelihood tree calculated with the combined plastid regions of *trnL-F* and *matK*, plus the 3' portion of the *trnK* intron for Schismatoglottideae. Posterior probability values (PP) are indicated above branches and likelihood bootstrap values (ML) are indicated below branches. Scale bar indicates the expected number of substitutions per site. Taxa in bold are rheophytes. Bold lines at the top left indicated the West Sarawak and Supra-Lupar Line clades.

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*'

*josefii* clade with weak support (ML 44%, PP 0.96). This clade was weakly supported as sister to *Phymatarum borneense* (Ar1442 + Ar1931) (PP 0.58). *Bakoa lucens* was embedded between the two accessions of *A. nicolsonii*, and *A. crassum* between two accessions of *B. motleyana*. There is increasing evidence that cpDNA regions are associated with geographic locations rather than to taxonomic relationships (Acosta and Premoli 2010; Palmé and Vendramin 2002; Jiménez et al. 2004). 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 monoplocenta* [Ar1966 + Ar1994], and *Aridarum 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 placentation (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

lower spathe orifice (character 10) and lower/spathe limb horizon (character 6) with RI = 0.553 and 0.545, respectively. Of the vegetative morphologies, shoot/root horizon disarticulation (character 1), and ligule senescence (character 3), received high RI values of 0.514 and 0.417, respectively. Ecological niches (character 17) and habit (character 18) received RI values of 0.516 and 0.5, respectively.

**Morphological Characters Linked to Rheophytism**—Of the 19 morphological, ecological and geological characters investigated (Fig. 3), it is proposed that the primary mechanisms that are adaptive for rheophytism radiation in Schismatoglottideae are: ability for root/shoot disarticulation (character 1), free ligular sheath (character 2), and marcescent ligule senescence (character 3). Secondly, erect infructescence orientation (character 13), and presence of a micropylar appendage on the seed (character 16), and thirdly, flaring lower spathe during anthesis (character 9), and basal placentation (character 11), and lastly, presence of thecae horns (character 12).

(CHARACTER 1) ROOT/SHOOT DISARTICULATION—The ability of the leafy shoot to disarticulate from the root system is apomorphic in *Cryptocoryne* + Schismatoglottideae (excluding *Apoballis*), with reversals in *Lagenandra* and *Schismatoglottis*. The disarticulation ability is an adaptation to aquatic or amphibious (*Cryptocoryne*), or rheophytic (Schismatoglottideae) habitats. Following stream flow, the disarticulated shoots lodge further downstream and are capable of regenerating roots, thus allowing for vegetative propagation. The abandoned shoot-stump was also capable of regenerating new shoots in less than three days (Fig. 4C). In addition, the leafy shoots were also able to shed drag induced by buffeting spathe flow (Fig. 4B).

(CHARACTER 2) PETIOLAR SHEATH ATTACHMENT—The leaf base is sheathing, generally for about one third to three fifths the length of the petiole. Petiolar sheath morphology in Schismatoglottideae is one of the primary characters used to define the subsets of the taxa studied.

A fully attached petiolar sheath is plesiomorphic for the Schismatoglottid Alliance. In Schismatoglottideae, the derivation of a free ligular sheath is homoplastic. *Apoballis*,

TABLE 2. Parsimony reconstruction (unordered) steps, likelihood reconstruction scores with model MK1 (est.), consistency index and retention index of 19 morphological, ecological and geological characters optimized onto 50% majority consensus rule tree from Bayesian analysis of 77 *trnL-F* and *matK*, plus the 3' portion of the *trnK* intron sequences of Schismatoglottideae, Cryptocoryneae, Philonotieae, and outgroup taxa.

Character	Parsimonious steps	$-\ln L$	Consistency index	Retention index
Geology	37	134.539	0.162	0.32
Inflorescence posture	28	94.277	0.107	0.306
Lower spathe dispersal mechanics	27	112.043	0.259	0.444
Infructescence orientation	25	70.163	0.08	0.324
Ecological niches	24	113.451	0.292	0.516
Post anthetic lower spathe orifice	20	83.018	0.15	0.553
Habit	20	92.430	0.25	0.5
Leaf blade position	20	67.448	0.1	0.333
Spathe limb senescence	19	61.821	0.105	0.227
Shoot/root disarticulation	18	52.519	0.056	0.514
Lower/ spathe limb horizon	17	64.159	0.118	0.545
Petiolar sheath attachment	17	66.861	0.118	0.4
Thecae horn	13	38.774	0.077	0.368
Micropylar appendage	12	38.415	0.083	0.5
Posterior costae	11	35.318	0.091	0.167
Placentation	10	36.386	0.1	0.735
Ligule senescence	9	34.304	0.222	0.417
Lower spathe movement during anthesis	8	41.503	0.25	0.143
Seeds	7	31.251	0.143	0.818

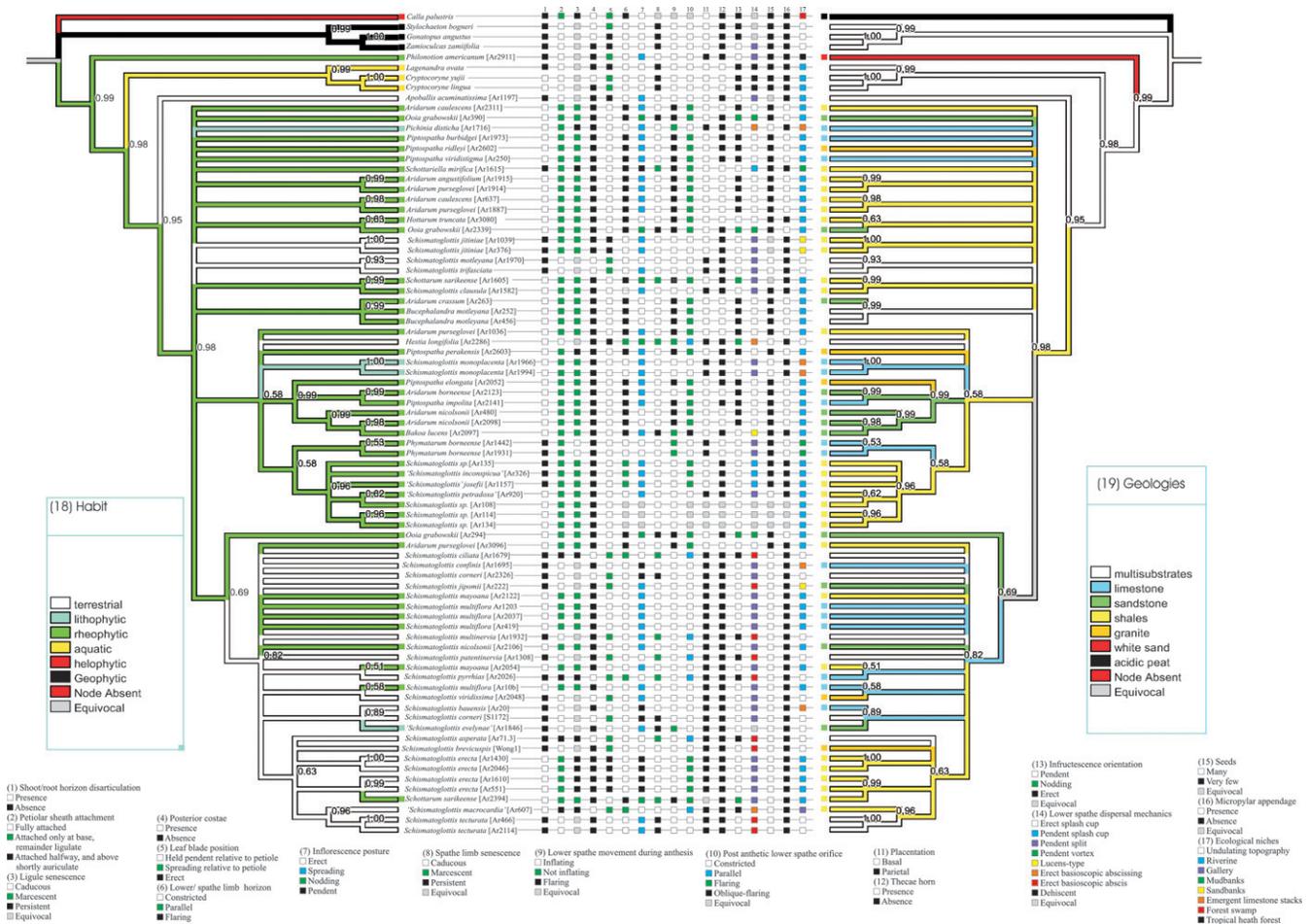


FIG. 3. Morphological, ecological, and geological characters mapped onto the 50% majority consensus rule Bayesian tree based on the combined plastid regions of *trnL-F* and *matK*, plus the 3' portion of the *trnK* intron for Schismatoglottideae, Cryptocoryneae, Philonotieae, and outgroup taxa. Characters are represented by numbers (1–19), please refer to Table 1 for character names. Character states are represented in different colors.

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 *Philonotium* (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

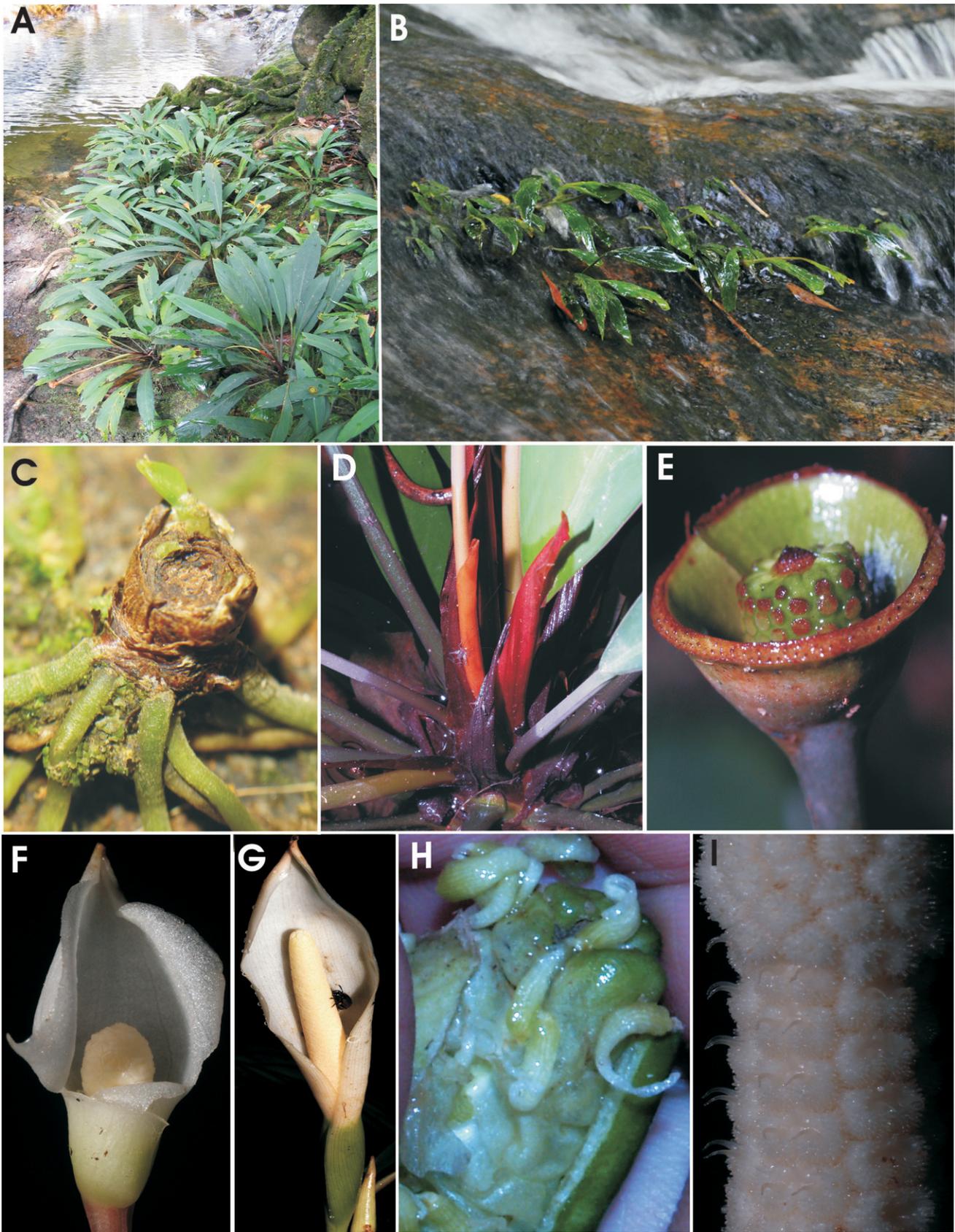


FIG. 4. A. *Piptospatha elongata* (Engl.) N. E. Br. in habitat. B. *Piptospatha perakensis* (Engl.) Ridl. plants in habitat. C. Shoot renewal post shoot/root disarticulation in *Aridarum borneense* (M. Hotta) Bogner & A. Hay. D. Marcescent ligular sheath in *Piptospatha elongata*. E. Splash-cup infructescence in *Piptospatha viridistigma* S. Y. Wong, P. C. Boyce & Bogner. F. Inflating lower spathe during anthesis in *Bucephalandra motleyana* Schott. G. Inflorescence of *Schismatoglottis multiflora* Ridl. during anthesis. H. Micropylar appendages on seeds of *Phymatarum borneense* M. Hotta. I. pairs of thecae horns of *P. borneense*.

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 declinate 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 declinate (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 abscising 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. maelii* 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. *Aridarum* and *Bucephalandra* are mainly caducous, although *Aridarum* 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 salviform through the

flaring of the lower spathe at the onset of female anthesis. *Aridarum* shows similar but somewhat less marked flaring; *Aridarum* inflorescences tend to open more slowly than those of *Piptospatha*. *Bakoa lucens*, in many respects, parallels the limb mechanics of *Apoballis* 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 spathes, 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 placenta 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. monoplocenta* M. Hotta has only one placenta (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. 4I) 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 thecae 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. *Caulescencia* M. Hotta. The last is presently an unresolved polytomy that does not cluster with *Aridarum* s. s. Thecae 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*, thecae horns are positioned laterally, either two on one side of the thecae directed into the thecae excavation, or one ventral and one dorsal with the end of the thecae excavation (Bogner and Hay 2000). Thecae horns in *Bucephalandra* and *Phymatarum* are uniformly slender needle-like structures arising from differentiated globose to ellipsoid thecae. In *Schottariella*, thecae 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) INFRACTESCENCE 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 *Bakoa* 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 recurves 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 acroscopic 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 recurves, 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 basicopically 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 placentation.

(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 *Bakoa*, and *Schottariella* (Boyce and Wong 2008). Micropylar appendage morphology is not uniform. Observations of their functionality 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. monoplocenta* and *S. bauensis* (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 predominantly 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 *Schismatoglottis* Multiflora Group. Taxa such as *S. monoplocenta* and *S. bauensis* are obligate lithophytes and also chasmophytic. However, most rheophytes in the Multiflora Group, and many in the “small” genera, while lithophytic tend to favor inclined rather than vertical slopes. Many lithophytic Schismatoglottideae are found growing in soil or debris-filled crevices. Exceptions include *B. lucens* and *A. crassum* which habitually grow on bare rock and display several adaptive features to enable them to grow in a particularly harsh environment, including sub-succulent leaf blades with thickened waxy cuticles, and disproportionately extensive root systems.

(CHARACTER 19) GEOLOGY—Geology is possibly the least well-studied ecological aspect of the Araceae. The relative abundance of limestone studies in Malaysia (Kiew et al. 2004) reveals only limited information about Araceae, even though they are an important element of this ecology. Although limestone aroid floras provide much information for the study of vicariance and evolutionary processes, other geologies are as rich, or indeed richer. In recent years, studies focusing on shales and granite, have begun to reveal a wealth of geologically endemic taxa. Granite provides a difficult habitat for species because it is both acidic and intrinsically impermeable to moisture, so that run-off in periods of heavy rain is intense and takes much in the way of nutrient and soil cover away with it. Conversely, in periods of dry weather, granite can become dry and where exposed, hot. Given these factors, it is not surprising that granite obligate species (e.g. *Piptospatha elongata*) are often endemic to localized areas.

Shales provide an acidic water-permeable habitat which degrades to form rich soil. Exposed shales in forests tend to be located in isolated patches and they also tend to be associated with water action. Therefore shale forests are frequently humid and provide an ideal habitat for both

mesophytes and rheophytes. Furthermore shale systems are frequently associated with isolated river systems (e.g. Song-Kanowit, Ai, Rejang drainages, etc.) and thus provide ecological isolation combined with geological specificity.

Sandstone habitats are the least uniform, and even in adjacent systems, can be variable in their composition. Good examples of ecological differences in sandstones leading to localized speciation are the Penrissen, Matang, Bako, and Santubong sandstones. In total, these extend no more than 100 km end to end, yet encompass three distinct sandstone geologies, separated from one another spatially. The Penrissen and Santubong series, while not related geologically, are similar in their morphology, both being fine grained and hard. The Matang series (including the Matang massif, Singgai, and Berendang, and across the Sarawak river the lower flanks of Muan [Serembon]) consist of large grains and for the most part are soft. Bako falls somewhere in the middle of these between the hardness of the Matang series and the superhard sandstones of Penrissen. The Penrissen range has species that are closely related to limestone obligate taxa suggesting that the Penrissen geology provides a habitat, in terms of edaphic conditions, that closely resembles that provided by limestones. The Santubong sandstones, while of similar hardness to those of Penrissen, harbor forests (and aroid species) different to those of Penrissen. One reason may be that Penrissen receives three times more rain per annum than Santubong. By contrast, the Matang series are water-permeable and the forest types (in the main MDF) reflect this with high canopy and a rich riverine flora. On its coastal side Bako receives more water than Santubong, but on the land side it is much drier. Furthermore, because it is not a high mountain, Bako seems less able to facilitate storm clouds directly above it and this may account for the marked floristic differences between Bako and Santubong.

Gallery 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. jitinia* S. Y. Wong, *S. 'bella'*, *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. trivitatta* 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 Schismatoglottideae 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 Schismatoglottideae seen today in Borneo. Where studies exist, Schismatoglottideae 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 functions 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: Homalomeneae), 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. ahmadii*, 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

- Acosta, M. C. and A. C. Premoli. 2010. Evidence of chloroplast capture in South American *Nothofagus* (subgenus *Nothofagus*, Nothofagaceae). *Molecular Phylogenetics and Evolution* 54: 235–242.
- Beccari, O. 1902. *Nelle foreste di Borneo*: 403, fig. 65, 524. Firenze: Tip. Di S. Landi.
- Beccari, O. 1904. *Wanderings in the great forests of Borneo*: 392. London: A. Constable and Co., Ltd.
- Bogner, J. 1983. A new *Hottarum* (Araceae) species from Borneo. *Plant Systematics and Evolution* 142: 49–55.
- Bogner, J. 1984a. On *Hapaline appendiculata* and *Phymatarum borneense*, two rare Araceae from Borneo. *Plant Systematics and Evolution* 145: 59–66.
- Bogner, J. 1984b. Two new Aroids from Borneo. *Plant Systematics and Evolution* 145: 159–164.
- Bogner, J. and A. Hay. 2000. Schismatoglottideae (Araceae) in Malesia 2: *Aridarum*, *Bucephalandra*, *Phymatarum* and *Piptospatha*. *Telopea* 9: 179–222.
- Boyce, P. C. 1994. New species of Araceae from Brunei. *Kew Bulletin* 49: 793–801.
- Boyce, P. C. and S. Y. Wong. 2006. Studies on Schismatoglottideae (Araceae) of Borneo I: A trio of new *Schismatoglottis* from Sarawak, Borneo. *Gardens' Bulletin Singapore* 58: 7–18.
- Boyce, P. C. and S. Y. Wong. 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.
- Boyce, P. C. and S. Y. Wong. 2008. Studies on Schismatoglottideae (Araceae) of Borneo VII: *Schottarum* and *Bakoa*, two new genera from Sarawak, Malaysian Borneo. *Botanical Studies (Taipei)* 49: 393–404.
- Boyce, P. C. and S. Y. Wong. 2009. *Schottariella mirifica* P.C. Boyce & S.Y. Wong: A new name for *Schottarum sarikeense* (Araceae: Schismatoglottideae) (Araceae: Schismatoglottideae) – an erratum. *Botanical Studies (Taipei)* 50: 269–271.
- Boyce, P. C., S. Y. Wong, and S. L. Low. 2012. Studies on Schismatoglottideae (Araceae) of Borneo XVII: The *Schismatoglottis hottae* Complex, a new informal taxon, and three new species from Sarawak, Malaysian Borneo. *Gardens' Bulletin Singapore*. 64: 257–269.
- Boyce, P. C., S. Y. Wong, S. L. Low, A. P. J. Ting, S. E. Low, I. H. Ooi, and K. K. Ng. 2010. Araceae of Borneo. *Aroideana* 33: 3–74.
- Bunting, G. S. 1960. The Genus *Schismatoglottis* (Section *Philonotium*) in America. *Annals of the Missouri Botanical Garden* 47: 69–71.
- Cabrera, L. I., G. A. Salazar, M. W. Chase, S. J. Mayo, J. Bogner, and P. Dávila. 2008. Phylogenetic relationships of aroids and duckweeds (Araceae) inferred from coding and noncoding plastid DNA. *American Journal of Botany* 95(9): 1153–1165.
- Croat, T. B. 1990. “1988”. Ecology and life forms of Araceae. *Aroideana* 11: 4–55.
- Croat, T. B. 1992. “1989”. Ecology and life forms of Araceae: A follow-up. *Aroideana* 12: 6–8.
- Croat, T. B., J. Whitehill, and E. D. Yates. 2007. A new subsection of *Anthurium* section *Calomystrium* (Araceae) and five new species from Colombia and Ecuador. *Aroideana* 30: 23–37.
- Cusimano, N., J. Bogner, S. J. Mayo, P. C. Boyce, S. Y. Wong, M. Hesse, W. Hettterscheid, R. C. Keating, and J. C. French. 2011. Relationships within the Araceae: Comparison of morphological patterns with molecular phylogenies. *American Journal of Botany* 98: 1–15.
- Hall, T. A. 1999. BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98.
- Hay, A. 1996. The genus *Schismatoglottis* Zoll. and Moritzi (Araceae: Schismatoglottideae) in Peninsular Malaysia and Singapore. *Sandakania* 7: 1–30.
- Hay, A. and Yuzammi. 2000. Schismatoglottideae (Araceae) in Malesia I – *Schismatoglottis*. *Telopea* 9: 1–177.
- Hotta, M. 1965. Notes on Schismatoglottinae of Borneo, I. *Memoirs of the College of Science, University of Kyoto, Series B* 32: 19–30.
- Hotta, M. 1966. Notes on Schismatoglottidinae of Borneo, II. *Memoirs of the College of Science, University of Kyoto, Series B* 33: 223–238.
- Hotta, M. 1976. Notes on Bornean plants III. *Pedicellarum* and *Heteroaridarum*, two new genera of the aroids. *Acta Phytotaxonomica et Geobotanica* 27: 61–65.
- Huelsensbeck, J. P. and F. Ronquist. 2001. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17: 754–755.
- Hutchison, C. S. 1989. *Geological Evolution of South-East Asia*. Oxford: Oxford University Press.
- Imaichi, R. and M. Kato. 1997. Speciation and morphological evolution in Rheophytes. Pp. 309–318 in *Evolution and diversification of land plants*, ed. K. Iwatsuki and P. H. Raven. Tokyo: Springer.
- Jiménez, P., U. López de Heredia, C. Collada, Z. Lorenzo, and L. Gil. 2004. High variability of chloroplast DNA in three Mediterranean

- evergreen oaks indicates complex evolutionary history. *Heredity* 93: 510–515.
- Kato, M. and R. Imaichi. 1992. A broad-leaved variant of the fern rheophytes, *Tectaria lobbii*. *International Journal of Plant Sciences* 153: 212–216.
- Kiew, R., C. Geri, J. Sang, and P. C. Boyce. 2004. The understory flora. *Sarawak Museum Journal* 80: 105–146.
- Low, S. L., S. Y. Wong, J. Jamliah, and P. C. Boyce. 2011. Phylogenetic study of the *Hottarum* Group (Araceae: Schismatoglottideae) by utilizing nuclear ITS region *Gardens' Bulletin Singapore* 63: 237–243.
- Maddison, W. P. and D. R. Maddison. 2010. Mesquite: A modular system for evolutionary analysis. Ver. 2.74. <http://mesquiteproject.org>.
- Mayo, S. J., J. Bogner, and P. C. Boyce. 1997. *The Genera of Araceae*. Kew: Royal Botanic Gardens.
- Meijaard, E. 2004. *Solving mammalian riddles. A reconstruction of the Tertiary and Quaternary distribution of mammals and their palaeoenvironments in island South-East Asia*. Unpubl. dissertation. Canberra: Australian National University.
- Mitsui, Y., S. T. Chen, Z. K. Zhou, C. I. Peng, Y. F. Deng, and H. Setoguchi. 2007. Phylogeny and biogeography of the genus *Ainsliaea* (Asteraceae) in the Sino-Japanese Region based on nuclear rDNA and plastid DNA sequence data. *Annals of Botany* 101: 111–124.
- Mori, Y. and H. Okada. 2001. Reproductive biology and pollen flow of a rheophytic aroid, *Furtadoa sumatrensis* (Araceae) in the Malesian wet tropics. *Plant Systematics and Evolution* 227: 37–47.
- Morrison, D. A. 2007. Increasing the efficiency of searches for the maximum likelihood tree in a phylogenetic analysis of up to 150 nucleotide sequences. *Systematic Biology* 56: 988–1010.
- Moss, S. J. and M. E. J. Wilson. 1998. Biogeographic Implications of the Tertiary Paleogeographic evolution of Sulawesi and Borneo. Pp. 133–163 in *Biogeography and geological evolution of Southeast Asia*, eds. R. Hall and J. D. Holloway. Leiden: Backbuys Publishers.
- Nomura, M., H. Setoguchi, and T. Takaso. 2006. Functional consequences of stenophylly for leaf productivity: Comparison of the anatomy and physiology of a rheophyte, *Farfugium japonicum* var. *luchense*, and a related non-rheophyte, *F. japonicum* (Asteraceae). *Journal of Plant Research* 119: 645–656.
- Okada, H. 2006. A new species of *Aridarum*, Schismatoglottideae, Araceae from the Muller Range, Central Kalimantan, Indonesia. *Acta Phytotaxonomica et Geobotanica* 57: 61–64.
- Okada, H. and Y. Mori. 2000. Three new species of Schismatoglottideae, Araceae, from Borneo. *Acta Phytotaxonomica et Geobotanica* 51: 1–9.
- Palmé, A. E. and G. G. Vendramin. 2002. Chloroplast DNA variation, postglacial recolonization and hybridization in hazel, *Corylus avellana*. *Molecular Ecology* 11: 1769–1779.
- Pollard, B. J. and A. Paton. 2001. A new rheophytic species of *Plectranthus* L'Hér. (Labiatae) from the Gulf of Guinea. *Kew Bulletin* 56: 975–982.
- Posada, D. 2008. jModelTest: Phylogenetic model averaging. *Molecular Biology and Evolution* 25: 1253–1256.
- Raes, N., M. C. Roos, J. W. Ferry Slik, E. Emiel van Loon, and H. ter Steege. 2009. Botanical richness and endemism patterns of Borneo derived from species distribution models. *Ecography* 32: 180–192.
- Razafimandimbison, S. G., J. Moog, H. Lantz, U. Maschwitz, and B. Bremer. 2005. Re-assessment of monophyly, evolution of myrmecophytism, and rapid radiation in *Neonaucla* s. s. (Rubiaceae). *Molecular Phylogenetics and Evolution* 34: 334–354.
- Ridley, H. N. 1893. On the flora of the eastern coast of the Malay Peninsula. *Transactions of the Linnean Society of London. 2nd series. Botany* 3: 267–408.
- Slik, J. W. Ferry, N. Raes, N. Shin-Ichiro, F. Q. Brearley, C. H. Cannon, E. Meijaard, H. Nagamasu, R. Nilus, G. Paoli, A. D. Poulsen, D. Sheil, E. Suzuki, J. L. C. H. van Valkenburg, C. O. Webb, P. Wilkie, and S. Wulffraat. 2009. Environmental correlates for tropical tree diversity and distribution patterns in Borneo. *Diversity & Distributions* 15: 523–532.
- Sonké, B., D. Neuba, D. Kenfack, and P. D. Block. 2007. An extraordinary new rheophyte in the genus *Leptactina* (Rubiaceae, Pavetteae) from Rio Muni (Equatorial Guinea). *Botanical Journal of the Linnean Society* 153: 109–113.
- Stamatakis, A., P. Hoover, and J. Rougemont. 2008. A rapid bootstrap algorithm for the RAxML Web-servers. *Systematic Biology* 57: 758–771.
- Swofford, D. L. 2002. PAUP\*: Phylogenetic analysis using parsimony (\* and other methods), version 4.0 beta 10. Sunderland: Sinauer Associates.
- Tyukaya, H. 2002. Leaf anatomy of a rheophyte, *Dendranthema yoshinaganthum* (Asteraceae), and of hybrids between *D. yoshinaganthum* and a closely related non-rheophyte species, *D. indicum*. *Journal of Plant Research* 115: 329–333.
- Tyukaya, H., R. Imaichi, and J. Yokoyama. 2006. Leaf-shape variation of *Paederia foetida* in Japan: Re-examination of the small, narrow leaf form from Miyajima Island. *Journal of Plant Research* 119: 303–308.
- Usukura, M., R. Imaichi, and M. Kato. 1994. Leaf morphology of a facultative rheophyte, *Fargugium japonicum* var. *luchense* (Compositae). *Journal of Plant Research* 107: 263–267.
- van Steenis, C. G. G. J. 1981. *Rheophytes of the world: an account of the flood-resistant flowering plants and ferns and the theory of autonomous evolution*. Alpena aan den Rijn, and Rockville: Sijthoff & Noordhoff.
- van Steenis, C. G. G. J. 1987. Rheophytes of the world. Supplement. *Allertonia* 4(Supplement): 267–330.
- van Welzen, P. C. and J. W. F. Slik. 2009. Patterns in species richness and composition of plant families in the Malay Archipelago. *Blumea* 54: 166–171.
- Wong, K. M. 1998. Patterns of plant endemism and rarity in Borneo and the Malay Peninsula. Pp. 139–169 in *Rare, threatened, and endangered Floras of Asia and the Pacific Rim, Academia Sinica, Monograph Series* 16, eds. Peng C. I. and P. P. Lowry. Taipei: Institute of Botany.
- Wong, S. Y. 2010. Studies on Schismatoglottideae (Araceae) of Borneo XII: Three new species of *Schismatoglottis* in the multiflora group. *Gardens' Bulletin Singapore* 61: 285–296.
- Wong, S. Y. and P. C. Boyce. 2007. Studies on Schismatoglottideae (Araceae) of Borneo V: Preliminary ecological observations of *Schismatoglottis* on the Matang Massif. *Aroidiana* 30: 71–81.
- Wong, S. Y. and P. C. Boyce. 2010a. Studies on Schismatoglottideae (Araceae) of Borneo IX: A new genus, *Hestia*, and resurrection of *Apoballis*. *Botanical Studies (Taipei)* 51: 249–255.
- Wong, S. Y. and P. C. Boyce. 2010b. Studies on Schismatoglottideae (Araceae) of Borneo XI: *Ooia*, a new genus and a new generic delimitation of *Piptospatha*. *Botanical Studies (Taipei)* 51: 543–552.
- Wong, S. Y. and P. C. Boyce. 2010c. Studies on Schismatoglottideae (Araceae) of Borneo X: *Pichinia*, a remarkable novel genus from Sarawak, Malaysian Borneo. *Gardens' Bulletin Singapore* 61: 297–304.
- Wong, S. Y., P. C. Boyce, A. S. Othman, and C. P. Leaw. 2010. Molecular phylogeny of tribe Schismatoglottideae based on two plastid markers and recognition of a new tribe, Philonotieae, from the Neotropics. *Taxon* 59: 117–124.

APPENDIX 1. Taxonomic position, herbarium voucher number, collection locality, and GenBank accession number of all the taxa included in the phylogenetic analysis of tribe Schismatoglottideae together with sequences available from GenBank [Taxa are arranged alphabetically following the taxonomic position of Bogner and Hay (2000), Hay and Yuzammi (2000), Wong and Boyce (2010a, b, c) and Wong et al. (2010)]. Combinations in single quotation marks have not been made and generic placements in these instances are inferred. Species, taxonomic position, collection locality, collectors, herbarium voucher no. and, GenBank accession no. (*trnL-F*, *matK*) – = not available

*Apoballis acuminatissima* Schott, *Apoballis*, cultivated, origin unknown, J. Bogner Ar1197 (SAR)/ BOGNER 2913 (M), GQ220977, GQ220907; *Aridarum borneense* (M. Hotta) Bogner & A. Hay, *Aridarum* section *Aridarum*, Sg. Bungen, Kubah National Park, Matang, Sarawak, 01.36 N, 110.11 E, P. C. Boyce et al. Ar2123 (SAR), GQ220954, GQ220886; *Aridarum caulescens* M. Hotta, *Aridarum* section *Caulescentia*, Bukit Satiam, Bintulu, Sarawak, 02.59 N, 112.56 E, P. C. Boyce & K. Jeland Ar637 (SAR), GQ220955, GQ220887; *Aridarum caulescens* M. Hotta, *Aridarum* section *Caulescentia*, Melinau Gorge, Mulu National Park, Nanga Medamit, Limbang, Miri, Sarawak, P. C. Boyce et al. Ar2311 (SAR), JN177480, JN177490; *Aridarum caulescens* var. *angustifolium* Bogner & Nicolson, *Aridarum* section *Caulescentia*, Batu Anchau trail, Similajau National Park, Bintulu, Sarawak, 03.21 N, 113.09 E, P. C. Boyce et al. Ar1915 (SAR), GQ220956, GQ220888; *Aridarum crassum* S. Y. Wong & P. C. Boyce, *Aridarum* section *Aridarum*, Gunung Gaharu, Pantu, Sri Aman, Sarawak, 01.01 N, 110.53 E, P. C. Boyce & K. Jeland Ar263 (SAR), GQ220957, GQ220889; *Aridarum nicolsonii* Bogner, *Aridarum* section *Aridarum*, Camp Permai, Santubong, Kuching, Sarawak, 01.46 N, 110.19 E, P. C. Boyce et al. Ar480 (SAR), JN177481, JN177491; *Aridarum nicolsonii* Bogner, *Aridarum* section *Aridarum*, Trail to Teluk Tajor, Bako National Park, Kuching, Sarawak, 01.43 N, 110.27 E, P. C. Boyce & S. Y. Wong Ar2098 (SAR), GQ220958, GQ220890; *Aridarum purseglovei* (Furtado) M. Hotta, *Aridarum* section *Caulescentia*, Bukit Satiam, Bintulu, Sarawak, 02.59 N, 112.56 E, P. C. Boyce et al. Ar1887 (SAR), GQ220960, GQ220892; *Aridarum purseglovei* (Furtado) M. Hotta, *Aridarum* section *Caulescentia*, Sungai Likau, GT Plantations, Tatau, Bintulu, Sarawak, 02.44 N, 113.25 E, P. C. Boyce et al. Ar3096 (SAR), JN177483, JN177493;

- Aridarum purseglovei* (Furtado) M. Hotta, *Aridarum* section *Caulescentia*, Batu Anchar trail, Similajau National Park, Bintulu, Sarawak, 03. 21 N, 113.09 E, P. C. Boyce et al. Ar1914 (SAR), GQ220961, GQ220893; *Aridarum purseglovei* (Furtado) M. Hotta, *Aridarum* section *Caulescentia*, Pelagus rapids, Pelagus, Kapit, Sarawak, 02. 11 N, 113. 03 E, P. C. Boyce et al. Ar1036 (SAR), GQ220959, GQ220891; *Bakoa lucens* P. C. Boyce & S. Y. Wong, *Bakoa*, Trail to Teluk Tajor, Bako National Park, Kuching, Sarawak, 01.43 N, 110.27 E, P. C. Boyce & S. Y. Wong Ar2097 (SAR), GQ220962, GQ220894; *Bucephalandra motleyana* Schott, *Bucephalandra*, Borneo Height, Padawan, Serian, Sarawak, 01.07 N, 110.13 E, P. C. Boyce & K. Jeland Ar456 (SAR), GQ220964, GQ220896; *Bucephalandra motleyana* Schott, *Bucephalandra*, Gunung Gaharu, Pantu, Sri Aman, Sarawak, 01.03 N, 110.53 E, P. C. Boyce & K. Jeland Ar252 (SAR), GQ220963, GQ220895; *Calla palustris* L., Outgroup, -, *Chase* 18102 (K), AM933363, AM920641; *Cryptocoryne lingua* Becc. ex. Engl., locality not known, *Chase* 10998 (K), AM920601, AM933329; *Cryptocoryne yuiji* Bastm., Outgroup, Trail from Kuala Terikan to Camp 5, Mulu National Park, Mulu, Miri, Sarawak, 04.13 N, 114.53 E, P. C. Boyce et al. Ar2321 (SAR), -, GQ220897; *Gonatopus angustus* N. E. Br., Outgroup, -, *Chase* 10675 (K), AM933328, AM920599; *Hestia longifolia* (Ridl.) S. Y. Wong & P. C. Boyce, *Hestia*, Sungai Abun Kiri, tributary from Sungai Terikan, from the back of Mentawai Research Station, Mulu National Park, Mulu, Miri, Sarawak, 04.14 N, 114.52 E, P. C. Boyce et al. Ar2286 (SAR), GQ220996, GQ220928; *Hottarum truncata* (M. Hotta) Bogner & Hay, *Hottarum*, Sungai Pandan Kecil, GT Plantations, Tatau, Bintulu, Sarawak, 02.43 N, 113.2 E, P. C. Boyce et al. Ar3080 (SAR), JN177482, JN177492; *Lagenandra ovata* (L.) Thwaites, Outgroup, locality not known, *Chase* 10991 (K), AM920602, AM933330; *Ooia grabowskii* (Engl.) S. Y. Wong & P. C. Boyce, *Ooia*, Nanga Gaat, Kapit, Sarawak, 01.45 N, 113.28 E, P. C. Boyce et al. Ar390 (SAR), GQ220974, GQ220904; *Ooia grabowskii* (Engl.) S. Y. Wong & P. C. Boyce, *Ooia*, Pergunungan Hose, Kapit, Sarawak, 02.15 N, 113.41 E, P. C. Boyce & K. Jeland Ar294 (SAR), GQ220973, GQ220903; *Ooia grabowskii* (Engl.) S. Y. Wong & P. C. Boyce, *Ooia*, Sungai Bungen, Kubah National Park, Matang, Kuching, Sarawak, 01.36 N, 110.12 E, I. H. Ooi Ar2339 (SAR), JN177484, JN177494; *Philonotion americanum* (A.M.E.Jonker & Jonker) S. Y. Wong & P. C. Boyce, French Guiana, J. Bogner, BOGNER 2911 (M), GQ220978, GQ220908; *Phymatarum borneense* M. Hotta, *Phymatarum*, Belaga Road, Sebauh, Bintulu, Sarawak, 03.03 N, 113.42 E, P. C. Boyce et al. Ar1442 (SAR), GQ220969, GQ220899; *Phymatarum borneense* M. Hotta, *Phymatarum*, Trail to Deer Cave, Mulu National Park, Mulu, Miri, Sarawak, 04.02 N, 114.49 E, P. C. Boyce et al. Ar1931 (SAR), GQ220970, GQ220900; *Pichinia disticha* S. Y. Wong, *Pichinia*, Sugun Karang, Gunung Kedadum, Pichin, Serian, Samarahan, Sarawak, 01.06 N, 110.29 E, P. C. Boyce et al. Ar1761 (SAR), GQ220986, GQ220917; *Piptospatha burbidgei* (N. E. Br.) M. Hotta, *Piptospatha* Elongata Group, Trail to Long Langsat, Sg. Licat, Mulu National Park, Mulu, Miri, Sarawak, 04.00 N, 114.49 E, P. C. Boyce et al. Ar1973 (SAR), GQ220971, GQ220901; *Piptospatha elongata* (Engl.) N. E. Br., *Piptospatha* Elongata Group, Gunung Gaharu, Pantu, Sri Aman, Sarawak, 01.01 N, 110.53 E, P. C. Boyce & S. Y. Wong Ar2052 (SAR), GQ220972, GQ220902; *Piptospatha impolita* (Engl.) N. E. Br., *Piptospatha* Elongata Group, Bukit Kankar, Sg. Limau, Sempadi, Lundu, Kuching, Sarawak, 01.40 N, 109.60 E, P. C. Boyce et al. Ar2141 (SAR), GQ220975, GQ220905; *Piptospatha perakensis* Ridl., *Piptospatha*, Lap 16, Bukit Larut Forest Reserve, Taiping, Perak, 04.48 N, 100.45 E, I. H. Ooi Ar2603 (SAR), JN177485, JN177495; *Piptospatha ridleyi* N. E. Br. ex Hook. f., *Piptospatha*, NERC to Visitor Complex, Endau Rompin National Park, Johor, 02.54 N, 103.42 E, I. H. Ooi Ar2602 (SAR), JN177486, JN177496; *Piptospatha viridistigma* P. C. Boyce & S. Y. Wong, *Piptospatha* Elongata Group, Gunung Gaharu, Pantu, Sri Aman, Sarawak, 01.03 N, 110.53 E, P. C. Boyce & K. Jeland Ar250 (SAR), GQ220976, GQ220906; *Schismatoglottis macrocardia*, *Asperata* Complex, Bukit Satiam, Bintulu, Sarawak, 02.59 N, 112.56 E, P. C. Boyce & K. Jeland Ar607 (SAR), JN177487, JN177497; *Schismatoglottis asperata* Engl., *Asperata* Group, Trail to Indian Temple, Matang, Kuching, Sarawak, 01.35 N, 110.13 E, P. C. Boyce & K. Jeland Ar71.3 (SAR), GQ220979, GQ220909; *Schismatoglottis bauensis* A. Hay & C. Lee, Multiflora Group, Bukit Batu, Jambusan, Bau, Kuching, Sarawak, -, P. C. Boyce & K. Jeland Ar20 (SAR), GQ220980, GQ220910; *Schismatoglottis brevicuspis* Hook. f., *Asperata* Group, West Malaysia, Living collection from John Tan, Singapore, Wong 1 (SAR), GQ220981, GQ220911; *Schismatoglottis ciliata* A. Hay, *Asperata* Group, Sg. Umpuh, Pichin, Serian, Samarahan, Sarawak, 01.07 N, 110.27 E, P. C. Boyce et al. Ar1679 (SAR), GQ220982, GQ220913; *Schismatoglottis clausula* S. Y. Wong, Multiflora Group, Ulu Sarikei, Sarikei, Sarawak, 01.55 N, 111.30 E, P. C. Boyce et al. Ar1582 (SAR), GQ221014, GQ220949; *Schismatoglottis confinis* S. Y. Wong & P. C. Boyce, Multiflora Group, Kampung Sadir, Padawan, Samarahan, Sarawak, K. Simon Ar1695 (SAR), GQ220983, GQ220914; *Schismatoglottis corneri* A. Hay, Corneri Group, Camp 5, Mulu National Park, Mulu, Miri, Sarawak, 04.08 N, 114.54 E, P. C. Boyce et al. Ar2326 (SAR), GQ220985, GQ220916; *Schismatoglottis corneri* A. Hay, Corneri Group, Crocker Range, Sabah, -, Singapore Botanical Garden Living Collection No.19991172, GQ220984, GQ220915; *Schismatoglottis erecta* M. Hotta, Multiflora Group, km 10 Bakun - Bintulu-Miri road junction, Belaga, Kapit, Sarawak, 02.51 N, 114.02 E, P. C. Boyce et al. Ar2046 (SAR), GQ220989, GQ220921; *Schismatoglottis erecta* M. Hotta, Multiflora Group, Nanga Sumpa, Batang Ai, Lubok Antu, Sri Aman, Sarawak, 01.12 N, 112.03 E, P. C. Boyce et al. Ar551 (SAR), GQ220987, GQ220922; *Schismatoglottis erecta* M. Hotta, Multiflora Group, Sg. Matob, Maradong, Sarikei, Sarawak, 01.52 N, 111.55 E, P. C. Boyce et al. Ar1610 (SAR), GQ220988, GQ220920; *Schismatoglottis erecta* M. Hotta, Multiflora Group, km 10 Bakun - Bintulu-Miri road junction, Belaga, Kapit, Sarawak, 02.51 N, 114.02 E, P. C. Boyce et al. Ar1430 (SAR), GQ220990, GQ220919; *Schismatoglottis evelynae*, *Tectura* Group, Sg. Bong, Kg. Tringgus, Krokong, Bau, Kuching, Sarawak, 01.16 N, 110.06 E, P. C. Boyce et al. Ar1846 (SAR), GQ220991, GQ220923; *Schismatoglottis inconspicua*, Multiflora Group, Nanga Gaat, Kapit, Sarawak, 01.42 N, 113.31 E, P. C. Boyce et al. Ar326 (SAR), GQ220992, GQ220924; *Schismatoglottis jipomi* P. C. Boyce & S. Y. Wong, *Tectura* Group, Segong, Bau, Kuching, Sarawak, 01.32 N, 110. 09 E, K. Jeland Ar222 (SAR), GQ220993, GQ220925; *Schismatoglottis jitiniae* S. Y. Wong, Multiflora Group, Nanga Gaat, Kapit, Sarawak, 01.45 N, 113.29 E, P. C. Boyce et al. Ar376 (SAR), GQ220994, GQ220926; *Schismatoglottis jitiniae* S. Y. Wong, Multiflora Group, Pelagus rapids, Pelagus, Kapit, Sarawak, 02.11 N, 113.03 E, P. C. Boyce et al. Ar1039 (SAR), GQ220995, GQ220927; *Schismatoglottis josefii* A. Hay, Multiflora Group, Sg. Pedali, Nanga Sumpa, Batang Ai, Lubok Antu, Sri Aman, Sarawak, 01.12 N, 112.03 E, P. C. Boyce et al. Ar1157 (SAR), GQ221012, GQ220947; *Schismatoglottis mayoana* Bogner & M. Hotta, Multiflora Group, Kubah National Park, Matang, Kuching, Sarawak, 01.36 N, 110.11 E, A. S. Lee & I. H. Ooi Ar2054 (SAR), GQ220997, GQ220929; *Schismatoglottis mayoana* Bogner & M. Hotta, Multiflora Group, Sg. Bungen, Kubah National Park, Matang, Kuching, Sarawak, 01.36 N, 110.12, P. C. Boyce et al. Ar2122 (SAR), GQ220998, GQ220930; *Schismatoglottis monoplacenta* M. Hotta, Multiflora Group, Trail from Clearwater Cave, Mulu National Park, Mulu, Miri, Sarawak, 04.03 N, 114.49 E, P. C. Boyce et al. Ar1966 (SAR), GQ220999, GQ220931; *Schismatoglottis monoplacenta* M. Hotta, Multiflora Group, Trail to and beyond Clearwater Cave, Mulu National Park, Mulu, Miri, Sarawak, 04.04 N, 114.50 E, P. C. Boyce et al. Ar1994 (SAR), GQ221000, GQ220932; *Schismatoglottis motleyana* (Schott) Engl., *Calyptrata* Group, Trail from Clearwater Cave, Mulu National Park, Mulu, Miri, 04.04 N, 114.50 E, P. C. Boyce et al. Ar1970 (SAR), GQ221001, GQ220933; *Schismatoglottis multiflora* Ridl., Multiflora Group, Gunung Br'aang, Padawan, Samarahan, Sarawak, 01.11 N, 110.10 E, P. C. Boyce & K. Jeland Ar10b (SAR), GQ221002, GQ220938; *Schismatoglottis multiflora* Ridl., Multiflora Group, Kampung Duyoh, Bau, Kuching, Sarawak, 01.21 N, 110.03 E, P. C. Boyce & K. Jeland Ar1203 (SAR), -, GQ220939; *Schismatoglottis multiflora* Ridl., Multiflora Group, Kubah National Park, Matang, Kuching, Sarawak, 01.36 N, 110.11 E, A. S. Lee & I. H. Ooi Ar2069 (SAR), -, GQ220935; *Schismatoglottis multiflora* Ridl., Multiflora Group, Recreational Park Ranchan, Serian, Samarahan, Sarawak, 01.09 N, 110.35 E, P. C. Boyce & S. Y. Wong Ar2037 (SAR), GQ221004, GQ220934; *Schismatoglottis multiflora* Ridl., Multiflora Group, Sg. Boyuh, Kg. Jugan, Bau, Kuching, Sarawak, K. Jeland & T. Jipom, Ar419 (SAR), GQ221003, GQ220936; *Schismatoglottis multinervia* M. Hotta, *Asperata* Group, Trail to Deer Cave, Mulu National Park, Mulu, Miri, Sarawak, 04.02 N, 114.49 E, P. C. Boyce et al. Ar1932 (SAR), GQ221005, GQ220940; *Schismatoglottis nicolsonii* A. Hay, Multiflora Group, Santubong, Kuching, Sarawak, 01.45 N, 110.20 E, P. C. Boyce et al. Ar2106 (SAR), GQ221006, GQ220941; *Schismatoglottis patentinervia* Engl., *Asperata* Group, Tubih, Pichin, Serian, Samarahan, Sarawak, 01.07 N, 110.27 E, P. C. Boyce et al. Ar1308 (SAR), GQ221007, GQ220942; *Schismatoglottis petradoxa*, Multiflora Group, Ulu Sarikei, Sarikei, Sarawak, 01.55 N, 111.30 E, P. C. Boyce et al. Ar1599 (SAR), -, GQ220943; *Schismatoglottis pyrrihins* A. Hay, *Asperata* Group, Bukit Sarang, Tatau, Bintulu, Sarawak, J. Leong-Skornickova et al. Ar2026 (SAR)/JLS-142 (SING), GQ221008, GQ220944; *Schismatoglottis sarikeensis* (Bogner & M. Hotta) A. Hay & Bogner, Multiflora Group, Sungai Lepong, Sarikei, Sarawak, 01.57 N, 111.31 E, P. C. Boyce et al. Ar1605 (SAR), JN177498, JN177498; *Schismatoglottis sarikeensis* (Bogner & M. Hotta) A. Hay & Bogner, Multiflora Group, Sungai Pedali, Nanga Sumpa, Batang Ai, Lubok Antu, Sri Aman, Sarawak, 01.12 N, 112.03 E, P. C. Boyce et al. Ar2394 (SAR), JN177489, JN177499; *Schismatoglottis sp.*, Multiflora Group,

Nanga Gaat, Kapit, Sarawak, 01.42 N, 113.26 E, P. C. Boyce & K. Jeland Ar134 (SAR), GQ221013, GQ220948; *Schismatoglottis* sp., Multiflora Group, Sg. Piat, Nanga Gaat, Kapit, Sarawak, 01.38 N, 113.24 E, P. C. Boyce & K. Jeland Ar108 (SAR), GQ221010, GQ220945; *Schismatoglottis* sp., Multiflora Group, Sg. Piat, Nanga Gaat, Kapit, Sarawak, 01.38 N, 113.24 E, P. C. Boyce & K. Jeland Ar114 (SAR), GQ221011, GQ220946; *Schismatoglottis tectorata* (Schott) Engl., Tectorata Group, Batu Taring, Singai, Bau, Kuching, Sarawak, K. Jeland & T. Jipom Ar466 (SAR), GQ221016, GQ220951; *Schismatoglottis tectorata* (Schott) Engl., Tectorata 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), AM933332, 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, Sarikei, 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.