

# Molecular phylogeny of tribe Schismatoglottideae (Araceae) based on two plastid markers and recognition of a new tribe, Philonotieae, from the neotropics

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**Abstract** Tribe Schismatoglottideae comprises one large genus, *Schismatoglottis*, and six small ‘satellite’ genera. A combined molecular phylogenetic analysis of *matK*, the 3′ portion of the *trnK* intron, and *trnL-F* sequence data was carried out on 77 taxa representing all genera in the tribe, all informal groups in *Schismatoglottis*, together with sister tribe Cryptocoryneae, and outgroups from Araceae. Analyses of combined datasets with parsimony, maximum likelihood, and Bayesian methods revealed tribe Schismatoglottideae to be a polyphyletic assemblage. Neotropical *Schismatoglottis* is shown to be sister to the palaeotropical Schismatoglottideae + Cryptocoryneae. *Schismatoglottis acuminatissima* is a sister clade to the rest of the Schismatoglottideae. Palaeotropical *Schismatoglottis* is unsupported as a monophyletic genus. A new neotropical tribe of Araceae, Philonotieae S.Y. Wong & P.C. Boyce, sister to Cryptocoryneae + palaeotropical Schismatoglottideae, is proposed.

**Keywords** Araceae; molecular systematics; Philonotieae; Schismatoglottideae; taxonomy

## INTRODUCTION

The Araceae are predominantly tropical in distribution, with 90% of 110 genera, and 95% of ca. 4000 species restricted to the everwet or perhumid tropics. Tribe Schismatoglottideae (Aroideae) with ca. 150 species is almost 95% endemic to Borneo. The tribe consists of mainly mesophytes, rheophytes, lithophytes and chasmophytes. The largest genus in the tribe, *Schismatoglottis* Zoll. & Moritz, extends from Myanmar (Burma) to Vanuatu and from southern subtropical China to New Guinea, with an additional three species in the neotropics. The tribe also includes six small ‘satellite’ genera: *Aridarum* Ridl., *Bakoa* P.C. Boyce & S.Y. Wong, *Bucephalandra* Schott, *Phymatarum* M. Hotta, *Piptospatha* N.E. Br., and *Schottarum* P.C. Boyce & S.Y. Wong, all, with the exception of *Piptospatha*, endemic to Borneo.

Recent and on-going research on Schismatoglottideae (Okada & al., 1999; Bogner & Hay, 2000; Hay & Yuzammi, 2000; Hay, 2002; Hay & Hershovitch, 2003; Boyce & Wong, 2006, 2008; Wong & Boyce, 2007, 2008; Bogner & Boyce, 2009; Wong & al., 2009), has provided a stable species platform from which to test hypotheses of infra-tribal and inter-generic phylogenetic relationships.

Previous molecular phylogenetic studies focused on family-wide analyses of Araceae and only included two or three taxa from Schismatoglottideae. Barabé & al. (2004) indicated that Schismatoglottideae are not monophyletic but form a monophyletic clade with *Cryptocoryne balansae* Gagnep. Cabrera & al. (2008) maintained Schismatoglottideae and

Cryptocoryneae as monophyletic. However, the neotropical *Schismatoglottis* was not included in the analysis. The objectives of the current research are to produce an established and testable phylogeny for the tribe Schismatoglottideae using two plastid markers (*trnL-F*, *matK*) and to resolve the internal topology of *Schismatoglottis* and the currently recognized satellite genera.

## MATERIALS AND METHODS

**Sampling.** — 71 samples were newly sequenced (65 taxa from Schismatoglottideae, 3 from Cryptocoryneae, 3 from other Araceae) and analyzed together with 6 samples obtained from GenBank (Appendix). The samples represent each taxonomic group (sensu Hay & Yuzammi, 2000) of *Schismatoglottis*: Calyptrata Group (4 taxa), Multiflora Group (28 samples representing 16 taxa), Tecturata Group (4 samples representing 3 taxa), Asperata Group (6 taxa), Corneri Group (2 samples of 1 taxon), and Rupestris Group (1 taxon) and one neotropical taxon (*Schismatoglottis americana*). The satellite genera sampled follow the generic taxonomy of Bogner & Hay (2000): *Aridarum* sect. *Aridarum* (3 taxa), and *A.* sect. *Caulescentia* (5 samples representing 3 taxa), *Bakoa* (1 taxon), *Bucephalandra* (one species sampled from two localities), *Phymatarum* (one taxon, sampled from two localities), *Piptospatha* Elongata Group (4 taxa), and Grabowskii Group (2 samples representing 1 taxon), and *Schottarum* (1 taxon). Six taxa from the tribe Cryptocoryneae were sampled: *Cryptocoryne balansae* Gagnep.,

*C. ferruginea* Engl., *C. lingua* Becc. ex Engl., *C. uenoi* Yui Sasaki, *C. yujii* Bastm. and *Lagenandra ovata* (L.) Thwaites. Due to difficulty in DNA amplification, species used from tribe Cryptocoryneae differed slightly between the *trnL-F* and *matK* regions. Based on the family-wide analysis of Mayo & al. (1997), we have chosen *Aglaonema nitidum* (Jack) Kunth, *Anchomanes difformis* (Blume) Engl., *Dieffenbachia spruceana* Schott, *Hapaline benthamiana* Schott and *Homalomena insignis* N.E. Br. as outgroups.

**DNA extraction, PCR and sequencing.** — Total DNA was extracted using a modified version of the CTAB method (Doyle & Doyle, 1987) with the addition of PVP (PolyVinylPyrrolidone) in the DNA extraction following Gauthier & al. (2008). The *trnL-F* intergenic spacer was amplified from total DNA using primers e and f (Taberlet & al., 1991). PCR amplifications for the *matK* and the 3' portion of the *trnK* intron were carried out using the forward primer 19F (Gravendeel & al., 2001) and reverse primer 2R (Steele & Vilgalys, 1994). Two internal primers, 390F and 1236R (Cuénoud & al., 2002) were used for sequencing. Each PCR reaction contained 1.5 µL of DNA template (100 ng/ml to 200 ng/ml), 2–4 units of *Taq* polymerase (New England Biolabs, Ipswich, Massachusetts, U.S.A.), 0.2 µM of each primer, 1× buffer, 1.5 mM MgCl<sub>2</sub>, 0.1 mM dNTP (New England Biolabs), 0.2 mg/ml of BSA (bovine serum albumin, New England Biolabs), and sterile double deionized water to make up to 20 µL final volume. Amplification was performed with the following program: 1 min at 94°C; 35 cycles of 30 s at 94°C, annealing at 54°C–56°C for 30 s, 2 min at 72°C, and a final extension of 2 min at 72°C. Double-stranded PCR products were viewed on a 1% agarose gel, and bands were excised and purified using an Invitrogen gel extraction kit following protocols provided by the manufacturer. Single-stranded PCR products were viewed on a 1% agarose gel and purified using an Invitrogen PCR purification kit. Purified products were viewed on 0.8% agarose gel and quantified using a UV spectrometer before sequencing. Sequencing was performed on an ABI 3100 (Applied Biosystems, California, U.S.A.) automated DNA sequencer using the DYEnamic™ ET terminator cycle sequencing kit (Amersham Pharmacia Biotech, Sweden) according to the manufacturer's protocol.

**Phylogenetic analyses.** — Both 5' and 3' strands of *trnL-F* spacer and *matK* region sequences obtained were manually checked by eye, and then edited using the BioEdit v.5.0.6 (Hall, 1999). The forward and reverse sequences were assembled and contig using the same software. Initial alignment of sequences was conducted using the CLUSTAL X v.1.83 (Thompson & al., 1997), and subsequently corrected by eye in BioEdit. Phylogenetic analyses were performed with PAUP\* v.4.0b10 (Swofford, 2002) for maximum parsimony reconstruction. Both regions were analysed independently and in combination. Gaps were treated as missing data. One thousand random addition sequence replicates were conducted using tree bisection-reconnection (TBR) branch swapping, with MULTREES in effect, but holding only one tree per step and saving no more than 10 trees per replicate to minimize time swapping on suboptimal trees. A second round of TBR branch swapping was performed on trees collected by

the first analysis, saving up to 10,000 trees. Once this limit was reached, trees were swapped to completion. Successive weighting of resulting trees was carried out according to the rescaled consistency index using the maximum value (best fit) criterion, and a base weight of 1.0. This was followed by a heuristic search with 10 random sequence addition replicates, TBR branch swapping, again saving no more than 10 trees per replicate. All trees from these 10 replicates were swapped to completion, after which a further round of weighting was implemented. This process was repeated until the same tree length/rescaled consistency index was obtained twice in succession. Internal clade support was evaluated both with and without weighting with 1000 bootstrap replicates, using simple sequence addition and TBR branch swapping. No more than 15 trees were saved in each replicate and only groups that appear in 50% of the trees were retained.

GARLI v.0-942 (Genetic Algorithm for Rapid Likelihood Inference; Zwickl, 2006) was used for maximum likelihood (ML) inference. Both regions were analysed independently, and in combination. GARLI performs heuristic phylogenetic searches under the general time reversible (GTR) model of nucleotide substitution, with gamma distributed rate heterogeneity (G) and a proportion of invariant sites (I). Runs were started from independent random starting trees. Indels were excluded from the analysis. The analysis was repeated three times to detect potential incongruences originating from different starting conditions. Generation number was set to 5 million, but analysis stopped automatically when no new significantly better scoring topology was encountered. A maximum likelihood heuristic bootstrapping search was performed with 100 replicates. This was compared with the topologies and bootstrap values generated from RAxML (Randomized Axelerated Maximum Likelihood) through CIPRES portal (Stamatakis & al., 2008) for 100 replicates, repeated 10 times to generate 1000 replicates.

Bayesian phylogenetic analyses were performed in MrBayes v.3.1.2 (Huelsenbeck & Ronquist, 2001). The most suitable models of nucleotide substitution for each of the gene regions were selected in MrModeltest v.2.2 (Nylander, 2004). Both regions were analysed independently and in combination. In the combined analyses, model parameters were fitted independently for each separate data partitions. Four Markov Chains were run for 1,000,000 generations each, saving every 100th tree. The first 2500 trees sampled were discarded as burn-in, and a 50% majority rule consensus tree was calculated for the remaining 7500 trees. For the purpose of comparison with bootstrapping, the phylogenetic stability of the tree nodes was given as posterior probabilities. Bayesian analyses were repeated three times to assure parameter convergence.

## ■ RESULTS AND DISCUSSION

**Analysis of *trnL-F* spacer.** — The length of the region in the Schismatoglottideae ranged from 351 bp (*Schismatoglottis mutata*) to 415 bp (*Schismatoglottis longifolia*), while in Cryptocoryneae it was 189 bp. Within Cryptocoryneae, a 234

bp gap was inserted from position 59 to 292. Following alignment of *trnL-F*, 439 characters were included, of which 61 (14%) are variable, and 40 (9%) are parsimony informative. 40 parsimony-informative characters resulted in a tree length of 159 steps with a consistency index (CI) of 0.79 and a retention index (RI) of 0.71. (Table 1)

**Analysis of the *matK* region.** — Following alignment of the region, 1615 characters were included in the analysis of which 168 (10%) are variable and 119 (7%) parsimony informative. The 119 parsimony informative characters resulted in a tree length of 383 steps, CI of 0.82 and RI of 0.81 (Table 1).

**Analysis of combined regions.** — 77 taxa were included in the combined regions analyses with taxa having only one region coded as missing data. A total of 419 most parsimonious trees has resulted with a tree length of 535 steps, CI of 0.79 and RI of 0.78. The combined analysis produced a topology identical to the individual molecular trees from separate datasets. However, the maximum likelihood tree from *trnL-F* placed *Schismatoglottis monoplacenta* in a clade with Cryptocoryneae, without support. Separate GARLI and RAxML analyses generated maximum likelihood trees with similar topologies and although support values for the trees differ slightly, this is not considered significant.

*Schismatoglottis americana* forms a basal clade to Schismatoglottideae + Cryptocoryneae (parsimony bootstrap value, BS<sub>PA</sub> 100%; likelihood bootstrap value, BS<sub>ML</sub> 100%; posterior probability, PP 1.00) (Fig. 1). Tribe Cryptocoryneae is strongly supported as a monophyletic clade (BS<sub>PA</sub> 83%, BS<sub>ML</sub> 92%, PP 1.00) basal to the rest of Schismatoglottideae with the exception of *S. americana* (BS<sub>PA</sub> 70%, BS<sub>ML</sub> 77%, PP 0.97). *Schismatoglottis acuminatissima* is a sister clade to the rest of the Schismatoglottideae (BS<sub>PA</sub> 62%, BS<sub>ML</sub> 61%, PP 0.99). The remainder of Schismatoglottideae is supported as a monophyletic clade (BS<sub>PA</sub> 73%, BS<sub>ML</sub> 79%, PP 1.00). However, *Schottarum sarikeense*, *S. jittinae*, and *S. disticha* remain as polytomies. The *Schismatoglottis* sensu stricto clade does not receive any support value. *Schismatoglottis corneri* is weakly supported as sister to the rest of *Schismatoglottis*.

Within the weakly supported satellite genera clade, the *Schismatoglottis josefii* complex remains a strongly supported clade (BS<sub>PA</sub> 88%, BS<sub>ML</sub> 86). This clade is nested within the *Schismatoglottis* sp. Ar1582, *S. petradoxa* and *Phymatarum borneense* clade, although not highly supported (PP 0.66). The *Bucephalandra motleyana* + *Aridarum crassum* clade receives better support (BS<sub>PA</sub> 100%, BS<sub>ML</sub> 92%). Unfortunately, the internal topology of the satellite genera and a few probably related *Schismatoglottis* species remains unresolved.

**Table 1.** Summary of characteristics for the datasets analysed in the *trnL-F*, *matK* and combined regions.

Dataset	No. of aligned characters	No. (%) of variable/informative characters	Tree length	CI/RI
<i>trnL-F</i>	439	61 (14%)/40 (9%)	159	0.79/0.71
<i>matK</i>	1615	168 (10%)/119 (7%)	383	0.82/0.81
Combined	2051	231 (11%)/157 (8%)	535	0.79/0.78

Exclusion of the neotropical '*Schismatoglottis*' renders Schismatoglottideae monophyletic; however, *Schismatoglottis* remains polyphyletic. The placement of several taxa of *Schismatoglottis* within the satellite genera is poorly supported. However, based on molecular and morphological evidence several taxa deserve formal recognition.

## ■ TAXONOMIC CONCLUSIONS

The molecular data presented here no longer support the placement of *Schismatoglottis americana* in *Schismatoglottis*, but the recognition of a new tribe for the neotropical '*Schismatoglottis*'.

Current taxonomy provides a generic name, *Philonotion* Schott, for neotropical *Schismatoglottis*. Formerly *Philonotion* was considered allied to *Adelonema* Schott (= *Homalomena*) in subtribe Adeloneminae, part of Schott's Philodendron alliance (Schott, 1860). Engler (1876) dismantled Adeloneminae by transferring *Adelonema* to *Homalomena*, as *H. erythropus* (Mart. ex Schott) Engl., thus merging Adeloneminae into Homalomenaeae. At the time, *Philonotion* was transferred to Philodendreae (Philodendroideae) where it remained until Bunting (1960) transferred one of the species (*Philodendron spruceanum*) to *Schismatoglottis*, simultaneously creating a new section, *Philonotion*, to accommodate the neotropical *Schismatoglottis* taxa (*S. americana* A.M.E. Jonker & Jonker, *S. bolivarana* G.S. Bunting & Steyererm. & *S. spruceana* (Schott) Bunting).

*Philonotion* Schott is here resurrected, based on the type *P. spruceanum*, and the two additional species of neotropical *Schismatoglottis* are transferred to *Philonotion*. The genus *Philonotion* is currently considered to be the only genus of Philonotieae S.Y. Wong & P.C. Boyce, a tribe sister to Schismatoglottideae + Cryptocoryneae, and together these three tribes form the Schismatoglottid alliance. The use of informal alliances was established by Grayum (1990) and later utilized by French & al. (1995) and Mayo & al. (1997).

To date only one genus and three species are known in Philonotieae, compared to more than 150 species in Schismatoglottideae and ca. 79 in Cryptocoryneae (ca. 65 in *Cryptocoryne* and 14 in *Lagenandra*). According to Bunting (1960) and other neotropical aroid specialists (notably Thomas Croat) *Philonotion* occurs along stream banks in forest bordering savanna.

Most other taxa in the Schismatoglottid alliance are highly moisture dependent and for the most part occur in heavily shaded conditions, except for the rheophytic taxa of the satellite genera in the group. In the Asian tropics, diversity and abundance is highest in the everwet/perhumid lowlands and decreases dramatically above 900 m. Philonotieae species are the only members of the Schismatoglottid alliance occurring on white-sand habitats.

The term "para-rheophyte" is used here to indicate species with no clear morphological adaptations to rheophytism (stenophylly, disarticulation of vegetative units, dispersal mechanisms favouring water, etc.), but nonetheless occurring in habitats that are inundated on a regular basis.



**Fig. 1.** A maximum likelihood tree calculated with the combined regions sequence data. Numbers next to branches are BS<sub>PA</sub>/BS<sub>ML</sub>/PP. Taxa are based on the genera recognized by Hay & Yuzammi (2000), Bogner & Hay (2000) and Boyce & Wong (2008). Bars indicate the Schismatoglottid alliance.

**Key to the tribes of the Schismatoglottid alliance**

1. Aquatic or amphibious, rarely hyper-seasonal savanna evergreen or seasonally dormant herbs. Spathe either with a conspicuous lower kettle and a long straight tube with connate margins (*Cryptocoryne*) or shortly tubular and twisted. Fruit a dehiscent syncarp or pseudo-apocarp. Spathe limb deliquescing. . . . . **Cryptocoryneae**
1. Terrestrial evergreen mesophytes or rheophytes. Spathe various but never with a kettle and connate-margined tube and never twisted. Fruit a berry, usually fleshy, but very rarely drying papery leading to it being wind-dispersed. Spathe limb frequently shedding during anthesis. . . . . 2
2. Fruits with 1–2 seeds on each of its 2 parietal placentae. Peduncle conspicuously elongated, equally or often exceeding the petioles. Plants of white-sand soils . . . . . **Philonotieae**
2. Fruits with many seeds on a variety of placental positions; if parietal then 3-placental; if seeds few then there are always more than 4 and always on a basal placenta. Peduncle usually shorter than the petioles, if equaling or exceeding then inflorescence nodding. Plants of a variety of habitats but never on white sand . . . . . **Schismatoglottideae**

**Philonotieae** S.Y. Wong & P.C. Boyce, **tr. nov.**

Herbae mesophytica vel para-rheophytica (vide infra) in habitatio campinarano (sylva tropicus subtempora super arenarius albis) crescenti. Caudice pleionanthico vel hapaxanthico. Folii lamina oblongo ad ovato, ad basin cuneatis vel ovatis vel cordatis. Pedunculo longiore quam petioli. Flores unisexuales, perigonio absentis, spatha constricta, lamina spathae caduca (semper?); spadice cum interstitio neutro plus minusve nudo cum staminodiis remotis tecto; ovario unilocularis, placentae 1–2, parietalis; ovulis 1–2 in quoque placentum. Fructus baccis. Seminis ignota. – Type: *Philonotion* Schott

Evergreen terrestrial mesophytic or para-rheophytic herbs with pleionanthic or hapaxanthic shoots. *Stem* hypogean or epigeal, erect to creeping. *Leaves* few to many; *petiole* terete; petiolar sheath fully attached, from 2/5 to 1/2 of the petiole length; *lamina* oblong to ovate, basally cuneate, ovate to cordate, apex often caudate and usually with a tubular mucro; primary venation pinnate, running to margin and there forming a prominent marginal vein, secondary venation parallel-pinnate; tertiary venation reticulate. *Inflorescences* solitary or in a 2-flowered synflorescence; *peduncle* exceeding the petioles; *spathe* constricted at junction of the lower part and limb, coinciding with a partially naked interstice and/or zone of sterile male flowers on the spadix, *lower spathe* tightly convolute, persistent into fruiting, limb caducous (always?) during anthesis; *spadix* sessile, flowers unisexual, aperigyniate; female flower zone partly adnate to the lower spathe; pistils crowded, distally sometimes interspersed with clavate interpistillar pistillodes, these exceeding the pistils; stigma discoid to hemispherical; ovary unilocular, placentae 1–2, parietal; ovules 1–2 per placenta, fusiform; sterile interstice with staminodes proximally, naked distally; male flower zone attenuate, stamens crowded, not obviously arranged into male

flowers; anthers truncate; thecae each opening an apical pore; appendix absent. *Fruiting* spathe urceolate; fruit berry; seeds 2–4, globose to ellipsoid, longitudinally costate.

*Distribution and habitat.* – Northeast South America: Colombia (Vaupes) through Venezuela (Bolívar and Amazonas) to the Guianas and into Northeast Brazil. Terrestrial mesophytes in savanna forest on white-sand or para-rheophytes on steep muddy river banks. Altitude below 400 m.

*Notes.* – Placentation in *Philonotion* is parietal as in *Schismatoglottis* (so far as known) but in *Philonotion* each placenta has only one or two ovules, and thus the unilocular ovary may contain one to four ovules. *Schismatoglottis* has three parietal placentae, each bearing many ovules. In *Philonotion* the spathe limb falls, probably during anthesis, (data lacking, as also on the condition of the limb at shedding), as it does in most *Schismatoglottis* and satellite genera, where the commonest state at shedding is caducous. *Philonotion* is a white-sand savanna genus, occurring in partial sun on white sandy soil but with abundant moisture present at the roots of plants, or occurring as para-rheophytes on steeply sloping, muddy banks of streams and subjected to periodic flooding.

***Philonotion*** Schott, Gen. Aroid.: 54. 1858 – Type: *Philonotion spruceanum* Schott.

Characters as for tribe.

1. ***Philonotion spruceanum*** Schott in Gen. Aroid.: 58. 1858 ≡ *Schismatoglottis spruceana* (Schott) Bunting in Ann. Missouri Bot. Gard. 47: 70. 1960.

*Distribution and habitat.* – Throughout the northern Amazon basin from Vaupés in Colombia to Amazonas in Venezuela and Brazil. The species occurs below 150 m a.s.l., usually on sandy soil, in full sun or partial shade (fide Croat & Lambert, 1986), as a terrestrial mesophyte in wet, white-sand savannas or on steep muddy river banks.

*Notes.* – Placentation in *P. spruceanum* is parietal. Stigmas in *P. spruceanum* turn pale orange post anthesis while male flowers are greenish before anthesis (Croat 59255, Venezuela, Amazonas, MO). Bunting (1960) reduced *Philonotion williamsii* Steyerl. to *Schismatoglottis spruceana* var. *williamsii*, differing only by having narrower leaf laminae and more slender petioles. *Schismatoglottis spruceana* var. *williamsii* occurs sympatrically with the typical variety.

2. ***Philonotion americanum*** (A.M.E. Jonker & Jonker) S.Y. Wong & P.C. Boyce, **comb. nov.** ≡ *Schismatoglottis americana* A.M.E. Jonker & Jonker in Acta Bot. Neerl. 2: 360. 1953.

*Distribution and habitat.* – Brazil (Amazonas), Colombia (Vaupes), French Guiana, Guyana, Surinam (Sipaliwini), Venezuela (Amazonas, Bolívar). On sandstone table mountains and along muddy banks of lowland forest streams, below 400 m a.s.l.

*Notes.* – When describing *Schismatoglottis americana*, A.M.E. Jonker-Verhoef & Jonker (1953) noted the possibility that their new species might have had to be moved into *Philonotion*. *Philonotion americanum* is distinguished by the

conspicuous long cuspidate (up to 2.5 cm long) lamina apex. The species has 2 parietal placentas and 4 ovules.

3. *Philonotium bolivaranum* (G.S. Bunting & Steyermark) S.Y. Wong & P.C. Boyce, **comb. nov.**  $\equiv$  *Schismatoglottis bolivariana* G.S. Bunting & Steyermark. in *Brittonia* 21(2): 187. 1969.

*Distribution and habitat.* – Venezuela (Bolívar, Amazonas). In white-sand savannas and on steep muddy river banks, 95–400 m a.s.l.

*Notes.* – *Philonotium bolivaranum* is the only neotropical species so far known with a cordate leaf base. Bunting & Steyermark (1969) noted that the lamina is silvery abaxially; however, in the latin diagnosis they described it as being abaxially greenish grey. Placentation in *P. bolivaranum* is elevated parietal.

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**Appendix.** Taxonomic position, herbarium voucher number, collection locality, and GenBank accession number of the species included in the phylogenetic analysis of tribe Schismatoglottideae. Taxa are arranged alphabetically following the taxonomic position of Bogner & Hay (2000), Hay & Yuzammi (2000) and Boyce & Wong (2008). 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

*Aglaoenema nitidum* (Jack) Kunth, Outgroup, Utak Manangi, Pichin, Serian, Samarahan, Sarawak, *Simon Kutuh ak Paru Ar941* (SAR), GQ220953, –; *Anchomanes difformis* (Blume) Engl., Outgroup, JBM (3991–84), *Barabé & Archambault 191* (MT), AY555186, GQ220885; *Aridarum borneense* (M. Hotta) Bogner & A. Hay, *Aridarum* sect. *Aridarum*, Sg. Bungen, Kubah National Park, Matang, Sarawak, 01°36'30.9"; 110°11'35.0", P.C. Boyce & al. *Ar2123* (SAR), GQ220954, GQ220886; *Aridarum caulescens* M. Hotta, *Aridarum* sect. *Caulescentia*, Bukit Satiam, Bintulu, Sarawak, 02°59'33.0"; 112°56'01.4", P.C. Boyce & Jeland ak Kisai *Ar637* (SAR), GQ220955, GQ220887; *Aridarum caulescens* var. *angustifolium* Bogner & Nicolson, *Aridarum* sect. *Caulescentia*, Batu Anchau trail, Similajau National Park, Bintulu, Sarawak, 03°20'52.7"; 113°09'29.8", P.C. Boyce & al. *Ar1915* (SAR), GQ220956, GQ220888; *Aridarum crassum* Wong S.Y. & P.C. Boyce, *Aridarum* sect. *Aridarum*, Gunung Gaharu, Pantu, Sri Aman, Sarawak, 01°01'19.5"; 110°52'52.8", P.C. Boyce & Jeland ak Kisai *Ar263* (SAR), GQ220957, GQ220889; *Aridarum nicolsonii* Bogner, *Aridarum* sect. *Aridarum*, Trail to Teluk Tajor, Bako National Park, Kuching, Sarawak, 01°43'03.1"; 110°26'42.7", P.C. Boyce & S.Y. Wong *Ar2098* (SAR), GQ220958, GQ220890; *Aridarum purseglovei* (Furtado) M. Hotta, *Aridarum* sect. *Caulescentia*, Pelagus rapids, Pelagus, Kapit, Sarawak, 02°11'15.1"; 113°03'29.01", P.C. Boyce & al. *Ar1036* (SAR), GQ220959, GQ220891; *Aridarum purseglovei* (Furtado) M. Hotta, *Aridarum* sect. *Caulescentia*, Bukit Satiam, Bintulu, Sarawak, 02°59'13.3"; 112°55'57.5", P.C. Boyce & al. *Ar1887* (SAR), GQ220960, GQ220892; *Aridarum purseglovei* (Furtado) M. Hotta, *Aridarum* sect. *Caulescentia*, Batu Anchau trail, Similajau National Park, Bintulu, Sarawak, 03°20'52.7"; 113°09'29.8", P.C. Boyce & al. *Ar1914* (SAR), GQ220961, GQ220893; *Bakoa lucens* P.C. Boyce & S.Y. Wong, *Bakoa*, Trail to Teluk Tajor, Bako National Park, Kuching, Sarawak, 01°43'03.1"; 110°26'42.7", P.C. Boyce & S.Y. Wong *Ar2097* (SAR), GQ220962, GQ220894; *Bucephalandra motleyana* Schott, *Bucephalandra*, Gunung Gaharu, Pantu, Sri Aman, Sarawak, 01°02'39.5"; 110°53'18.3", P.C. Boyce & Jeland ak Kisai *Ar252* (SAR), GQ220963, GQ220895; *Bucephalandra motleyana* Schott, *Bucephalandra*, Borneo Height, Padawan, Serian, Sarawak, 01°07'35.1"; 110°13'28.8", P.C. Boyce & Jeland ak Kisai *Ar456* (SAR), GQ220964, GQ220896; *Cryptocoryne balansae* Gagnep., Outgroup, locality not known, *Barabé & Archambault 203* (MT), AY555173, –; *Cryptocoryne ferruginea* Engl., Outgroup, Gunung Bidi, Bau, Kuching, Sarawak, 01°50'27.0"; 110°07'07.6", P.C. Boyce & Jeland ak Kisai *Ar943* (SAR), GQ220965, –; *Cryptocoryne lingua* Becc. ex Engl., locality not known, *Chase 10998* (K), AM920601, AM933329; *Cryptocoryne uenoi* Yuji Sasaki, Outgroup, Sg. Wuak, Pakan Wuak, Sarikei, Sarawak, 01°50'01.2"; 111°37'18.2", P.C. Boyce & al. *Ar1629* (SAR), GQ220966, –; *Cryptocoryne yujii* Bastm., Outgroup, Trail from Kuala Terikan to Camp 5, Mulu National Park, Mulu, Miri, Sarawak, 04°12'58.0"; 114°53'20.1", P.C. Boyce & al. *Ar2321* (SAR), –; GQ220897; *Dieffenbachia spruceana* Schott, Outgroup, Peru, Leg. S. Barrier, *Josef Bogner BOGNER 2954* (M), GQ220967, GQ220898; *Hapaline benthamiana* Schott, Outgroup, locality not known, *Chase 10676* (K), AM920609, AM933336; *Homalomena insignis* N.E. Br., Outgroup, Bukit Kankar, Sg. Limau, Sempadi, Lundu, Kuching, Sarawak, 01°39'44.2"; 109°59'56.5", P.C. Boyce & al. *Ar2145* (SAR), GQ220968, –; *Lagenandra ovata* (L.) Thwaites, Outgroup, locality not known, *Chase 10991* (K), AM920602, AM933330; *Phymatarum borneense* M. Hotta, *Phymatarum*, Belaga Road, Sebauh, Bintulu, Sarawak, 03°03'34.3"; 113°42'16.4", P.C. Boyce & al. *Ar1442* (SAR), GQ220969, GQ220899; *Phymatarum borneense* M. Hotta, *Phymatarum*, Trail to Deer Cave, Mulu National Park, Mulu, Miri, Sarawak, 04°02'23.8"; 114°48'54.6", P.C. Boyce & al. *Ar1931* (SAR), GQ220970, GQ220900; *Piptospatha burbridgei* (N.E. Br.) M. Hotta, *Piptospatha* *Elongata* Group, Trail to Long Langsat, Sg. Licat, Mulu National Park, Mulu, Miri, Sarawak, 04°00'03.5"; 114°48'49.8", P.C. Boyce & al. *Ar1973* (SAR), GQ220971, GQ220901; *Piptospatha elongata* (Engl.) N.E. Br., *Piptospatha* *Elongata* Group, Gunung Gaharu, Pantu, Sri Aman, Sarawak, 01°01'19.5"; 110°52'52.8", P.C. Boyce & S.Y. Wong *Ar2052* (SAR), GQ220972, GQ220902; *Piptospatha grabowskii* (Engl.) Engl., *Piptospatha* *Grabowskii* Group, Pergunungan Hose, Kapit, Sarawak, 02°14'47.2"; 113°41'24.9", P.C. Boyce & Jeland ak Kisai, *Ar294* (SAR), GQ220973, GQ220903; *Piptospatha grabowskii* (Engl.) Engl., *Piptospatha* *Grabowskii* Group, Nanga Gaat, Kapit, Sarawak, 01°44'44.5"; 113°28'32.3", P.C. Boyce & al. *Ar390* (SAR), GQ220974, GQ220904; *Piptospatha impolita* (Engl.) N.E. Br., *Piptospatha* *Elongata* Group, Bukit Kankar, Sg. Limau, Sempadi, Lundu, Kuching, Sarawak, 01°39'44.2"; 109°59'56.5", P.C. Boyce & al. *Ar2141* (SAR), GQ220975, GQ220905; *Piptospatha viridistigma* P.C. Boyce & S.Y. Wong, *Piptospatha* *Elongata* Group, Gunung Gaharu, Pantu, Sri Aman, Sarawak, 01°02'39.5"; 110°53'18.3", P.C. Boyce & Jeland ak Kisai *Ar250* (SAR), GQ220976, GQ220906; *Schismatoglottis acuminatissima* Schott, *Rupestis* Group, cultivated, origin unknown, *Josef Bogner Ar197* (SAR)/ *BOGNER 2913* (M), GQ220977, GQ220907; *Schismatoglottis americana* A.M.E. Jonker & Jonker, French Guiana, *Josef Bogner BOGNER 2911*, GQ220978, GQ220908; *Schismatoglottis asperata* Engl., *Asperata* Group, Trail to Indian Temple, Matang, Kuching, Sarawak, 01°35'25.7"; 110°13'12.8", P.C. Boyce & Jeland ak Kisai *Ar71.3* (SAR), GQ220979, GQ220909; *Schismatoglottis bauensis* A. Hay & C. Lee, *Multiflora* Group, Bukit Batu, Jambusan, Bau, Kuching, Sarawak, P.C. Boyce & Jeland ak Kisai *Ar20* (SAR), GQ220980, GQ220910; *Schismatoglottis brevicuspis* Hook. f., *Asperata* Group, West Malaysia, living collection from John Tan, Singapore, *Wong 1* (SAR), GQ220981, GQ220911; *Schismatoglottis calyptrata* (Roxb.) Zoll. & Moritz, *Calypttrata* Group, JBM (3568–85), *Barabé & Chantha 89*, AY555172, –; *Schismatoglottis ciliata* A. Hay, *Asperata* Group, Sg. Umpuh, Pichin, Serian, Samarahan, Sarawak, 01°07'24.2"; 110°27'07.7", P.C. Boyce & al. *Ar1679* (SAR), GQ220982, GQ220913; *Schismatoglottis confinis* S.Y. Wong & P.C. Boyce, *Multiflora* Group, Kampung Sadir, Padawan, Samarahan, Sarawak, *Simon Kutuh ak Paru Ar1695* (SAR), GQ220983, GQ220914; *Schismatoglottis corneri* A. Hay, *Corneri* Group, Crocker Range, Sabah, No.19991172, Singapore Botanical Garden Living Collection, GQ220984, GQ220915; *Schismatoglottis corneri* A. Hay, *Corneri* Group, Camp 5, Mulu National Park, Mulu, Miri, Sarawak, 04°08'11.8"; 114°53'36.3", P.C. Boyce & al. *Ar2326* (SAR), GQ220985, GQ220916; *'Schismatoglottis disticha'*, *Multiflora* Group, Sugun Karang, Gunung Kedadam, Pichin, Serian, Samarahan, Sarawak, 01°06'17.6"; 110°29'04.5", P.C. Boyce & al. *Ar1761* (SAR), GQ220986, GQ220917; *'Schismatoglottis dulosa'*, *Multiflora* Group, Kampung Jugan, Bau, Kuching, Sarawak, 01°28'46.4"; 110°05'08.5", P.C. Boyce & Jeland ak Kisai *Ar279* (SAR), –; GQ220918; *Schismatoglottis erecta* M. Hotta, *Multiflora* Group, Nanga Sumpa, Batang Ai, Lubok Antu, Sri Aman, Sarawak, 01°12'07.6"; 112°02'51.2", P.C. Boyce & al. *Ar551* (SAR), GQ220987, GQ220922; *Schismatoglottis erecta* M. Hotta, *Multiflora* Group, Sg. Matob, Maradong, Sarikei, Sarawak, 01°52'06.1"; 111°55'30.7", P.C. Boyce & al. *Ar1610* (SAR), GQ220988, GQ220920; *Schismatoglottis erecta* M. Hotta, *Multiflora* Group, km 10 Bakun–Bintulu–Miri road junction, Belaga, Kapit, Sarawak, 02°50'51.7"; 114°01'57.6", P.C. Boyce & al. *Ar2046* (SAR), GQ220989, GQ220921; *Schismatoglottis erecta* M. Hotta; *Multiflora* Group, km 10 Bakun–Bintulu–Miri road junction, Belaga, Kapit, Sarawak, 02°50'51.7"; 114°01'57.6", P.C. Boyce & al. *Ar1430* (SAR), GQ220990, GQ220919; *'Schismatoglottis evelynae'*, *Tecturata* Group, Sg. Bong, Kg. Tringus, Krokong, Bau, Kuching, Sarawak, 01°15'32.2"; 110°05'37.2", P.C. Boyce & al. *Ar1846* (SAR), GQ220991, GQ220923; *'Schismatoglottis inconspicua'*, *Multiflora* Group, Nanga Gaat, Kapit, Sarawak, 01°42'01.1"; 113°31'14.8", P.C. Boyce & al. *Ar326* (SAR), GQ220992, GQ220924; *Schismatoglottis jipomi* P.C. Boyce & S.Y. Wong, *Tecturata* Group, Segong, Bau, Kuching, Sarawak, 01°32'00.9"; 110°08'58.8", *Jeland ak Kisai Ar222* (SAR), GQ220993, GQ220925; *'Schismatoglottis jitinae'*, *Multiflora* Group, Nanga Gaat, Kapit, Sarawak, 01°44'44.5"; 113°28'32.3", P.C. Boyce & al. *Ar376* (SAR), GQ220994, GQ220926; *'Schismatoglottis jitinae'*, *Multiflora* Group, Pelagus rapids, Pelagus, Kapit, Sarawak, 02°11'15.1"; 113°03'29.01", P.C. Boyce & al. *Ar1039* (SAR), GQ220995, GQ220927; *Schismatoglottis josefii* A. Hay, *Multiflora* Group, Sg. Pedali, Nanga Sumpa, Batang Ai, Lubok Antu, Sri Aman, Sarawak, 01°11'58.9"; 112°03'27.0", P.C. Boyce & al. *Ar1157* (SAR), GQ221012, GQ220947; *Schismatoglottis longifolia* Ridl., *Calypttrata* Group, Sungai Abun Kiri, tributary from Sungai Terikan, from the back of Mentawai Research Station, Mulu National Park, Mulu, Miri, Sarawak, 04°14'07.4"; 114°52'27.6", P.C.

## Appendix. Continued.

Boyce & al. *Ar2286* (SAR), GQ220996, GQ220928; *Schimatoglottis mayoana* Bogner & M. Hotta, Multiflora Group, Kubah National Park, Matang, Kuching, Sarawak, 01°35'40.2"; 110°10'45.9", *Lee Ai Shan & Ooi Im Hin Ar2054* (SAR), GQ220997, GQ220929; *Schimatoglottis mayoana* Bogner & M. Hotta, Multiflora Group, Sg. Bungen, Kubah National Park, Matang, Kuching, Sarawak, 01°36'30.9"; 110°11'35.0", *P.C. Boyce & al. Ar2122* (SAR), GQ220998, GQ220930; *Schimatoglottis monoplacenta* M. Hotta, Multiflora Group, Trail from Clearwater Cave, Mulu National Park, Mulu, Miri, Sarawak, 04°03'14.2"; 114°49'24.3", *P.C. Boyce & al. Ar1966* (SAR), GQ220999, GQ220931; *Schimatoglottis monoplacenta* M. Hotta, Multiflora Group, Trail to and beyond Clearwater Cave, Mulu National Park, Mulu, Miri, Sarawak, 04°04'01.6"; 114°49'45.2", *P.C. Boyce & al. Ar1994* (SAR), GQ221000, GQ220932; *Schimatoglottis motleyana* (Schott) Engl., Calyprata Group, Trail from Clearwater Cave, Mulu National Park, Mulu, Miri, 04°03'49.2"; 114°49'51.7", *P.C. Boyce & al. Ar1970* (SAR), GQ221001, GQ220933; *Schimatoglottis multiflora* Ridl., Multiflora Group, Bukit Manok, Padawan, Samarahan, Sarawak, 01°12'; 110°18', *P.C. Boyce & Jeland ak Kisai Ar10* (SAR), –, GQ220937; *Schimatoglottis multiflora* Ridl., Multiflora Group, Gunung Br'aang, Padawan, Samarahan, Sarawak, 01°11'; 110°10', *P.C. Boyce & Jeland ak Kisai Ar10b* (SAR), GQ221002, GQ220938; *Schimatoglottis multiflora* Ridl., Multiflora Group, Sg. Boyuh, Kg. Jugan, Bau, Kuching, Sarawak, *Jeland ak Kisai & Jipom ak Tisai, Ar419* (SAR), GQ221003, GQ220936; *Schimatoglottis multiflora* Ridl., Multiflora Group, Kampung Duyoh, Bau, Kuching, Sarawak, 01°20'45.6"; 110°02'36.9", *P.C. Boyce & Jeland ak Kisai Ar1203* (SAR), –, GQ220939; *Schimatoglottis multiflora* Ridl., Multiflora Group, Recreational Park Ranchan, Serian, Samarahan, Sarawak, 01°08'34.9"; 110°35'02.4", *P.C. Boyce & S.Y. Wong Ar2037* (SAR), GQ221004, GQ220934; *Schimatoglottis multiflora* Ridl., Multiflora Group, Kubah National Park, Matang, Kuching, Sarawak, 01°35'40.2"; 110°10'45.9", *Lee Ai Shan & Ooi Im Hin Ar2069* (SAR), –, GQ220935; *Schimatoglottis multinervia* M. Hotta, Asperata Group, Trail to Deer Cave, Mulu National Park, Mulu, Miri, Sarawak, 04°02'23.8"; 114°48'54.6", *P.C. Boyce & al. Ar1932* (SAR), GQ221005, GQ220940; *Schimatoglottis mutata* Hook. f., Rupestris Group, Thailand, *Croat 53521*, AY290846, –, *Schimatoglottis nicolsonii* A. Hay, Multiflora Group, Santubong, Kuching, Sarawak, 01°45'0.1"; 110°19'58.1", *P.C. Boyce & al. Ar2106* (SAR), GQ221006, GQ220941; *Schimatoglottis patentinervia* Engl., Asperata Group, Tubih, Pichin, Serian, Samarahan, Sarawak, 01°07'16.6"; 110°26'51.2", *P.C. Boyce & al. Ar1308* (SAR), GQ221007, GQ220942; '*Schimatoglottis petradoxa*', Multiflora Group, Ulu Sarikei, Sarikei, Sarawak, 01°55'05.4"; 111°29'35.8", *P.C. Boyce & al. Ar1599* (SAR), –, GQ220943; *Schimatoglottis pyrrhias* A. Hay, Asperata Group, Bukit Sarang, Tatau, Bintulu, Sarawak, *Jana Leong-Skornickova & al. Ar2026* (SAR)/JLS-142 (SING), GQ221008, GQ220944; *Schimatoglottis sp.*, Multiflora Group, Sg. Piat, Nanga Gaat, Kapit, Sarawak, 01°38'09.1"; 113°24'09.9", *P.C. Boyce & Jeland ak Kisai Ar108* (SAR), GQ221010, GQ220945; *Schimatoglottis sp.*, Multiflora Group, Sg. Piat, Nanga Gaat, Kapit, Sarawak, 01°38'09.1"; 113°24'09.9", *P.C. Boyce & Jeland ak Kisai Ar114* (SAR), GQ221011, GQ220946; *Schimatoglottis sp.*, Multiflora Group, Nanga Gaat, Kapit, Sarawak, 01°41'49.4"; 113°26'16.3", *P.C. Boyce & Jeland ak Kisai Ar134* (SAR), GQ221013, GQ220948; *Schimatoglottis sp.*, A. Hay, Multiflora Group, Ulu Sarikei, Sarikei, Sarawak, 01°55'05.4"; 111°29'35.8", *P.C. Boyce & al. Ar1582* (SAR), GQ221014, GQ220949; *Schimatoglottis tectorata* (Schott) Engl., Tectorata Group, Batu Taring, Singai, Bau, Kuching, Sarawak, *Jeland ak Kisai & Jipom ak Tisai Ar466* (SAR), GQ221016, GQ220951; *Schimatoglottis tectorata* (Schott) Engl., Tectorata Group, Kubah National Park, Matang, Kuching, Sarawak, 01°36'30.9"; 110°11'35.0", *P.C. Boyce & al. Ar2114* (SAR), GQ221015, GQ220950; *Schimatoglottis viridissima* A. Hay, Calyprata Group, Waterfall No. 1, Gunung Gading, Lundu, Kuching, Sarawak, 01°41'28.3"; 109°50'43.6", *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°52'06.1"; 111°55'30.7", *P.C. Boyce & al. Ar1615* (SAR), GQ221009, GQ220912.