Phylogenetic study of the *Schismatoglottis* Nervosa Complex (Araceae: Schismatoglottideae)

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ABSTRACT. The *Schismatoglottis* Nervosa Complex (Araceae: Schismatoglottideae) currently comprises 10 species: *Schismatoglottis adoceta* S.Y.Wong, *S. elegans* A.Hay, *S. liniae* S.Y.Wong, *S. tessellata* S.Y.Wong, *S. ulusarikeiensis* S.Y.Wong, *S. matangensis* S.Y.Wong, *S. simonii* S.Y.Wong, *S. turbata* S.Y.Wong, and *S. nervosa* Ridl., occurring in Borneo, with each endemic to a specific locality and most to a particular geology; and one species (*S. brevicuspis* Hook.f.) widespread in Peninsular Malaysia and Sumatera, where it is restricted to granites. Based on analysis of the *mat*K region, a preliminary biogeographical hypothesis for the origins and subsequent taxagenesis of the Nervosa Complex is presented. This study also provides insight into possible evolution of localised mesophytic endemics in everwet, humid, and perhumid megathermal Sundaic forests. Two clades are resolved: one north of, and another south of, the Lupar Divide.

Keywords. Araceae, biogeography, Borneo, *mat*K, *Schismatoglottis* Nervosa Complex, vicariance

Introduction

Geology and tectonics of Borneo

Borneo is the third largest island in the world and the second largest tropical island after New Guinea. Borneo is situated in a tectonically intricate region between three marginal basins: the South China, Sulu and Celebes Seas (Hall et al. 2008), the latter two on the eastern edge of the Sunda Shelf. Borneo has a complex geological history having been formed by Mesozoic accretion of oceanic crustal material (ophiolite), island arcs and microcontinental fragments accreted to the Palaeozoic continental core of the now Schwaner Mountains (Hutchison 1989; Moss & Wilson 1998; Hall et al. 2008). Despite this rather active formation, Borneo is now a stable area with little or no seismic activity, and has no active volcanoes (Hall 2002; Hall et al. 2008).

Plant endemism in Borneo

Borneo is frequently cited—rightly although nowadays somewhat repetitively—as one of the world's areas of 'mega'-biodiversity. With a flora comprising at least 3000

tree species alone (MacKinnon et al. 1996; Slik et al. 2003), Borneo's floristic patterns are significantly correlated with topography and geography (Slik et al. 2003). Present-day floristic patterns are probably influenced by Pleistocene glaciations and are suggested to be of recent emergence after the Pleistocene glacial period. The Southeast Asian mainland and Sumatera were formerly connected to Borneo by land bridges during the Pleistocene glacial (Morley 2000) and the emergence (more accurately, re-emergence) of lowland humid forest is almost certainly owing to rapid radiation of the relictual fragmentary floras from southeast Borneo (Meratus), and/or expansion of forest remnants from the Riau Pocket (see Corner 1960; Ashton 2005). It has also been suggested that Pleistocene refugia extended to north and northwest Borneo (Ashton 1972; Wong 1998), providing yet other points of taxon radiation.

It is estimated that c. 37% of Borneo's 15,000 vascular plant species are endemic (Roos et al. 2004; Welzen et al. 2005), although these figures are likely both underestimates given that studies are consistently revealing that a high percentage of the mesophytic flora appears to be endemic, and includes a great many novelties, e.g., the findings in Zingiberales alone: Theilade & Mood (1997, 1999), Nagamasu & Sakai (1999) and Takano & Nagamasu (2007).

Sabah and Sarawak together are frequently cited to have the most endemic plant species in Borneo, notably in mountainous areas (Moss & Wilson 1998). Frequently it is stated that much of the plant endemism of Borneo occurs in areas of the north, west Sarawak (notably), Sabah's Crocker Range (including Kinabalu) and Trusmadi Range, the central Bornean mountain chain (the Schwaner–Muller–Iran Range), and also in the southeastern Meratus range (Mackinnon et al. 1996). However, it is important to remember that the collecting density of much of highland Borneo is almost infinitesimally small, and thus the taxonomic wealth of the numerous smaller and isolated upland areas (e.g., the Kalimantan Kapuas Hilir, and flanking (Sarawak) Klingkang range, the Kapuas Hulu, Sambiliung, etc.) has yet to be sampled in any scientifically meaningful way. Furthermore, increasingly it is becoming apparent that the *lowland* areas have, despite their frequently degraded condition, still an extraordinary untapped reserve of novel taxa, many with highly restricted, often geologically obligate, ranges.

The *Schismatoglottis* Nervosa Complex

Since 2000, the genus *Schismatoglottis* has been the focus of attention aimed at resolving both its taxonomy and phylogeny (Hay & Yuzammi 2000). Wong (2010) delimitated the Nervosa complex by the presence of aromatic vegetative tissues (terpenoids), longitudinally ribbed petioles, and leaf blades with tessellate tertiary venation. Seven novel species additional to the two (*Schismatoglottis nervosa* and *S. elegans*) recognised by Hay & Yuzammi (2000) were proposed. In addition, *S. brevicuspis* was recognised as belonging to the Nervosa complex.

Thus, as now defined the Nervosa Complex comprises 10 described species. A further four species await description. *Schismatoglottis nervosa* and *S. elegans* are

restricted to Karst limestones in the southwest and northeast of Sarawak, respectively; *Schismatoglottis matangensis* and *S. turbata* are species of sandstones, with *S. matangensis* occurring on soft sandstones under perhumid moist forest, while *S. turbata* occurs in humid forest where it is restricted to the tops of small Bornhardts comprised of very hard sandstone. *Schismatoglottis adoceta*, *S. tessellata* and *S. ulusarikeiensis* are restricted to shales, *S. simonii* is unusual in that it occurs on both limestones (the type) and sandstones, while *S. liniae* and *S. brevicuspis* are granite obligates. Of the four species awaiting formal description, one is endemic to basalt in East Sabah, and one each to limestone at Mulu, shale in west Kapit, and limestone in southern central Bintulu.

This study investigates taxonomic relatedness within the Nervosa Complex and possible correlation between phytogeographical patterns and phylogeny of the complex, and presents a hypothesis of taxagenesis of the localised endemics.

Materials and methods

Sample collection and outgroup selection
The ingroup for the analysis consisted of 13 species (each with one accession, except for *S. simonii*, from two localities) from Sabah and Sarawak and one species from West Malaysia. Of these, 13 accessions were collected from the living collection at Semenggoh Botanical Research Centre, Kuching, Sarawak, and one accession was collected from Perak, Peninsular Malaysia, supplied through Universiti Sains Malaysia, Pulau Pinang (see Table 1). The outgroup taxon selected was *Apoballis acuminatissima* S.Y.Wong & P.C.Boyce, established as the Asian sister species to *Schismatoglottis* (Wong et al. 2010).

DNA extraction, PCR and sequencing
DNA was extracted from fresh samples using the protocol of Wong et al. (2010). The primers used for the *matK* gene region, which partially includes the 5' flanking region of the *trnK* intron were: *matK* 19F (Gravendeel et al. 2001), and *matK* 2R (Steele & Vilgalys 1994).

Polymerase Chain Reaction (PCR) amplifications were performed in a Biometra Tgradient thermal cycler. PCR conditions included an initial 2-min denaturation at 95°C, 35–40 cycles of 1 min at 95°C (denaturation), 1 min at 50–60°C (annealing), and 2 min at 72°C (extension), followed by a final 10-min extension at 72°C. PCR products were purified using a PureLink™ PCR Purification Kit (Invitrogen Corp.). The purified products were then sent to a commercial company for sequencing by including two internal primers: 390F and 1326R (Cuénoud et al. 2002).

Data analyses
Sequences were assembled and manually aligned using BioEdit Sequence Alignment Editor v7.0.5 (Hall 1999). Parsimony analysis was performed with PAUP* 4.0b10 (Swofford 2000) using PaupUp graphical interface (Calendini & Martin 2005) with

Table 1. GenBank accessions, vouchers and locality information for species of the *Schismatoglottis* Nervosa Complex (Araceae: Schismatoglottideae) in the present study.

Species	GenBank accession	Voucher no.	Location	Geology
Schismatoglottis simonii	JN570740	AR174	Sarawak, Serian, Gunung Ampungan	limestone
Schismatoglottis nervosa	JN570742	AR944	Sarawak, Bau, Gunung Bidi	limestone
Schismatoglottis tessellata	JN570748	AR1087	Sarawak, Kapit, Taman Rekreasi Sebabai	shales
Schismatoglottis adoceta	JN570739	AR1408	Sarawak, Kapit, Belaga	shales
Schismatoglottis ulusarikeiensis	JN570746	AR1579	Sarawak, Sarikei,Ulu Sarikei	shales
Schismatoglottis simonii	JN570751	AR1686	Sarawak, Serian, Mongkos	shales
Schismatoglottis matangensis	JN570741	AR1864	Sarawak, Matang, Kubah National Park	sandstone
Schismatoglottis elegans	JN570747	AR1877	Sarawak, Miri, Niah National Park	limestone
Schismatoglottis sp. nov. aff nervosa	JN570744	AR1930	Sarawak, Miri, Mulu	limestone
Schismatoglottis liniae	JN570743	AR2062	Sarawak, Lundu, Gunung Gading	granite
Schismatoglottis sp. nov. aff nervosa	JN570749	AR2078	Sarawak, Bintulu, Bukit Sarang	limestone
Schismatoglottis turbata	JN570750	AR2143	Sarawak, Lundu, Sempadi	sandstone
Schismatoglottis sp. nov. aff nervosa	JN570745	AR2482	Sabah, Tawau	basalt
Schismatoglottis brevicuspis	GQ220910	AR2677	Peninsular Malaysia, Perak	granite

all characters treated as "unord" and with equal weight. Gaps were treated as missing values. Random addition sequence was used as starting point and 10000 replicates retained. Branch-swapping was undertaken using the tree-bisection-reconnection (TBR) algorithm. No more than 3 trees of score (length) >/= to 1 were saved for each replicate. Steepest descent option was not in effect and branches were collapsed if maximum branch length was zero. The "MulTrees" option was in effect and topological constraints not enforced. 10000 bootstrap replicates were completed. The consistency index (CI), homoplasy index (HI), retention index (RI) and rescaled consistency index (RCI) were calculated with one of the most-parsimonious trees (MPTs).

Results

Unaligned sequences of the *matK* region of the ingroup taxa ranged from 1448 to 1740 bp. The final length for the aligned sequences comprised 1436 characters which

included two additions in *S. simonii* AR1686 (from 626 to 631bp) and *A. acuminatissima* (from 1505 to 1510bp). To align the sequences with the outgroup, 11 gaps were added. 3 variable sites were found from 200bp to 1400bp. From the 1436 bps, 1413 (98%) characters were constant, 14 (1%) of them were parsimony-uninformative and 9 (1%) of them were parsimony-informative characters.

One of 28 most parsimonious trees was selected (Fig. 1). There are two apparent clusters within the Nervosa Complex with weakly supported bootstrap values: *S. simonii* AR1686, *S. adoceta* AR1408, *S. tessellata* AR1087, *S.* sp. nov. aff. *nervosa* AR2078, *S. brevicuspis* AR2677, *S. ulusarikeiensis* AR1579 and *S. elegans* AR1877 (bootstrap 43%); and *S. nervosa* AR944, *S. simonii* AR174, *S. matangensis* AR1864, *S. liniae* AR2062, *S. turbata* AR2143, *S.* sp. nov. aff. *nervosa* AR1930 and AR2482 (bootstrap: 50%). Within these, however, *Schismatoglottis adoceta*, *S. brevicuspis*, *S. tessellata* and *S.* sp. nov. aff. *nervosa* AR2078 form a group with strong bootstrap support (100%), and this is weakly grouped (bootstrap: 36%) with *S. simonii* AR1686. *Schismatoglottis ulusarikeiensis* and *S. elegans* are sister to this clade (bootstrap: 64%). *Schismatoglottis nervosa*, *S. simonii* AR174, *S. matangensis*, *S. liniae* and *S. turbata* form a strongly supported clade (bootstrap: 100%). The *S.* sp. nov. aff. *nervosa* AR1930 and *S.* sp. nov. aff. *nervosa* AR2482 clade is also strongly supported (bootstrap: 100%).
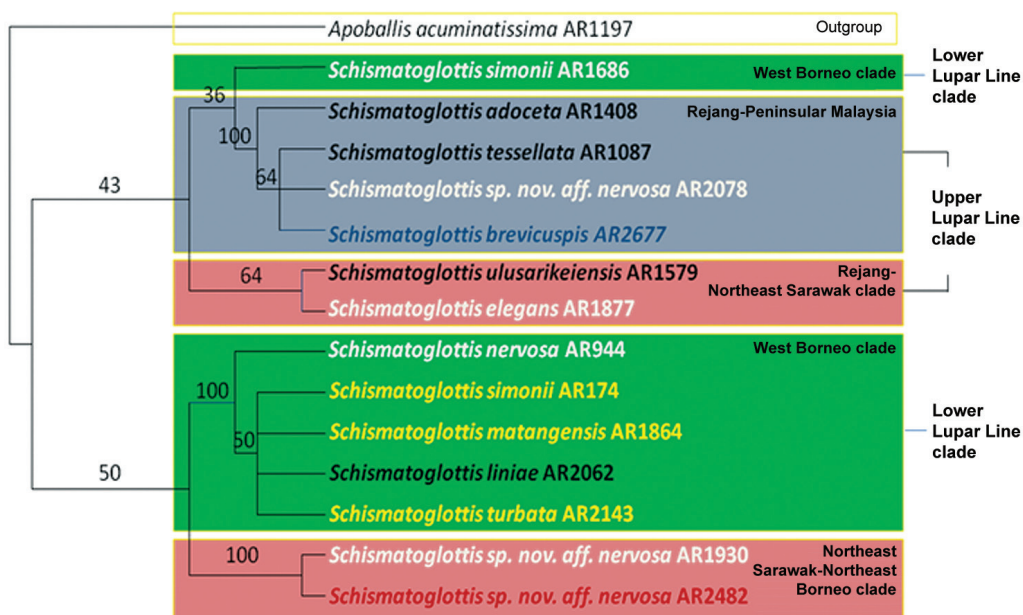

Fig. 1. One of 28 most parsimonious trees for the *Schismatoglottis* Nervosa complex based on the *matK* region. Tree length 26. Consistency index (CI) 0.885. Retention index (RI) 0.870. Rescaled consistency index (RC) 0.769. Homoplasy index (HI) 0.115. Although some clusters are weakly supported, potential clade relationships that may correspond to either side of the Lupar Line are indicated as hypotheses for continuing work.

Discussion

The Nervosa Complex comprises two general clusters: (((Rejang-Peninsular Malaysia), West Borneo) Rejang-NE Borneo) and (W Borneo, NE Sarawak-NE Borneo). Apparently, the cluster radiations are separated to below and above the Lupar Divide. The upper Lupar Divide clade comprises *S. adoceta* and *S. tessellata* (both Kapit, on shales)*, S.* sp. nov. aff. *nervosa* AR2078 (Bintulu)*,* and *S. elegans* in Miri. The Lower Lupar Line clade comprises *Schismatoglottis simonii* AR1686, *S. nervosa*, *S. simonii* AR174, *S. matangensis*, *S. liniae*, and *S. turbata*. The Lupar Line was an active convergent plate margin between the Late Cretaceous (65–99mya) to Palaeocene (54.8–65mya), with the margins extending through Engkilili and Lubok Antu (Tan 1979), approximately in line with the saddle that currently separates the Kapuas Hilir and Kapuas Hulu mountains. Hutchison (1996) stated that the sediments of the Lupar Line are the result of fluvial system deposition from the interior of a proto-Sundaland. The Lupar Formation comprises turbidites (deposits comprising rhythmic alternations of fine-grained, graded sandstones and shale beds) and igneous rocks (Honza et al. 2000). Active subduction of the oceanic crust occurred during the Cretaceous (65–144 mya) or early Tertiary (33.7–65 mya). The Rejang-Peninsular Malaysia clade (*S. adceta*, *S. tessellata* and *S.* sp. nov. aff. *nervosa* AR2078, *S. brevicuspis*), is estimated to have evolved from the last common ancestor during the Early Tertiary (33.7–65 mya). *Schismatoglottis adoceta*, *S. tessellata* and *S.* sp. nov. aff. *nervosa* AR2078 are in the Belaga and Lupar formations in Sarawak and Embaluh Group and Selangkai Formations in Kalimantan, circumscribed in the South by the Lupar Line ophiolite and in the North by the Bukit Mersing Line (Hutchison 1989), The Rajang Group comprises turbidite sedimentation dating from the Late Cretaceous (65–99 mya) to Late Eocene (33.7–41.3mya), formed by accretion at a subduction trench (Honza et al. 2000). Bedding dips are generally southward, but become younger northward. Our preliminary results also suggest that the Belaga might act as geographical barrier for the distribution of *S. simonii, S. tessellata, S.* sp. nov. aff. *nervosa* AR2078, and *S. adoceta.. Schismatoglottis adoceta* and *S. tessellata* are found on shales, whereas *S.* sp. nov. aff. *nervosa* AR2078 is locally restricted to limestones. The inclusion of *S. brevicuspis* (granite, Perak, Peninsular Malaysia) may be explicable as a relict of the former Riau Pocket flora (Corner 1960), running from present-day Terengganu to north-east Borneo, and might in former times have provided a corridor of everwet "stepping stones". Indeed, morphologically, *S. simonii* is morphologically proximate to *S.* sp. nov. aff. *nervosa* AR2078.

Schismatoglottis ulusarikeiensis is grouped with *S. elegans* to form the Rejang-NE Sarawak cluster/clade. *Schismatoglottis ulusarikeiensis* occurs on shales at Ulu Sarikei, while *S. elegans* is restricted to the Niah limestones at Gunung Subis, which are composed of limestone from the Tangap Formation (Hazebroek & Abang Kashim 2000). The southern part of the Niah system consists of sandstone from the Nyalau Formation. The Subis Limestone was formed by reefs, coralline algae and tiny shellfish of about 23 mya (Hazebroek & Abang Kashim 2000).

The West Borneo clade comprises *S. nervosa*, *S. simonii*, *S. matangensis*, *S. liniae* and *S. turbata*, and is considered be perhaps Middle Eocene (33.7–54.8 mya) in origin. The sediments on which two of the species (*S. matangensis* and *S. turbata*) occur are of Eocene origin (Moss & Wilson 1998). However, *S. nervosa* is restricted to the Bau Limestone, which are Upper Jurassic (180–206mya) (Wolfenden 1965), although its origin is dependent on when the Bau limestones emerged. *Schismatoglottis matangensis*, *S. simonii* AR174 and *S. turbata* are restricted to sandstones but on separate localities and differing ecologies: *S. matangensis* is found on soft sandstones under perhumid moist forest in Matang, Kuching, *S. simonii* AR174 on sandstone in Gunung Ampungan, Serian, while *S. turbata* is restricted to micro-Bornhardts comprised of very hard sandstone in Lundu. *Schismatoglottis liniae* is restricted to granite beneath perhumid forest at Gunung Gading, Lundu.

  Schismatoglottis sp. nov. aff. *nervosa* AR1930 is restricted to the Mulu limestones. The Mulu Formation comprises Palaeocene (54.8–65mya) to Eocene (33.7–54.8mya) miogeoclinal (non-volcanic) formations of limestone, sandstone, shale and slate (Hutchison 1989), suggesting the as-yet undescribed species might have evolved during the Eocene. *Schismatoglottis* sp. nov. aff. *nervosa* AR2482, is restricted to basalt outcrops at Bukit Quoin, Tawau (E Sabah), predominantly the result of young volcanism: the Tawau-Gunung Wullersdorf area is predominatly composed of basaltic-andesite which resembles the Pliocene (1.8–5.3mya) eruptions of the Mostyn Estate of Kunak (Hutchison 2005). Bukit Quoin is further considered a young volcanic edifice as the volcanic rocks have weathered only to a depth of 6m (Kirk 1962), suggesting that the volcanism of the Tawau area ceased during the Quaternary. Although *Schismatoglottis* sp. nov. aff. *nervosa* AR1930 and *S.* sp. nov. aff. *nervosa* AR2482 are sister taxa; *S.* sp. nov. aff. *nervosa* AR2482 occurs on the young basalts, suggesting an adaptation that may have occurred recently (probably during Pliocene or Pleistocene).

Conclusion

The *Schismatoglottis* Nervosa complex diversified in Borneo with one widespread species in West Malaysia to Sumatera. The Bornean local endemism of the complex is unique with each species being adapted to their geological localities. This seems to be correlated with speciation radiations and numerous vicariance events. Analyses of *matK* data resolves the *Schismatoglottis* Nervosa complex into two apparent clusters, one above and one below the Lupar Divide: a Rejang-Peninsular Malaysia clade and a W Borneo clade, with the exception of two species from NE Sarawak-NE Borneo that grouped with species from W Borneo. Recent and rapid radiation of the Nervosa Complex in Borneo is perhaps owing to vicariance events from spatial and temporal isolations, combined with geological and ecological factors. On-going analyses involving further gene regions and mapping of morphological and ecological data are being undertaken to better resolve incongruences.

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