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Geological Perambulations

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Figure 1. *Schismatoglottis multinervia* M.Hotta is restricted to limestone outcrops at Mulu N.P., NE Sarawak.

Figure 2. *Schismatoglottis hayi* S.Y.Wong & P.C.Boyce is closely similar to *S. multinervia*, and is found only on heavily forested limestone at Niah Caves N.P.

Of all ecologically significant factors, geology is possibly one of the least well-studied and documented, and certainly least well-understood aspects of tropical Araceae. By way of example, despite the relative abundance of limestone-related floristic studies in Malaysia (e.g., Ping & Kiew, 1997; Kiew *et al.*, 2004) these published accounts contain only limited information concerning Araceae, despite the fact that aroids constitute a major floristic element of the biodiversity of tropical limestones. Although data relating to aroid geological preferences are noted in various revisionary accounts for tropical Asia including for *Alocasia* (Hay, 1998, 1999), *Piptospatha* (Wong et al., 2009), and *Schismatoglottis* (Hay & Yuzammi, 2000; Wong 2010) so far only Boyce & Wong (2009) have published specifically on the aroids and their associated geology. The only other publication that we are aware of is from Brazil, another country with an enormously rich and diverse aroid flora, where Gonçalves (2010) published specifically on aroids and their geology. Nonetheless, fieldwork in Borneo over the past few years has begun to provide a wealth of data on the often highly localized species that are restricted to specific habitats.

To start with limestone formations, a particularly striking feature of these remarkable ecologies is that often a particular limestone outcrop harbours its own unique species, but other such formations have related but different species that are themselves locally unique. For example, *Schismatoglottis multinervia* M.Hotta (Figure 1), is unique to limestone formations at Mulu National Park in NE Sarawak and is most closely related to *S. hayi* S.Y.Wong & P.C.Boyce (Figure 2), a recently described species occurring only on the limestones at Niah Caves N.P., some 130 km to the west of Mulu. Other such examples of sibling species involving the extraordinarily rich Mulu limestones are *Alocasia reginae* N.E.Br. (Mulu – Figure 3) and *A. reginula* A.Hay (from Bukit Tabin, Sabah – Figure 4), and the even more complex situation presented by the Mulu endemic *Amorphophallus julaihii* Ipor, Tawan & P.C.Boyce (Figure 5) which is related to no fewer than four other species, each associated with a specific limestone area: *A. niahensis* P.C.Boyce & Hett. (Niah Cave N.P. – Figure 6), *A. juliae* P.C.Boyce & Hett. (Merirai, central Sarawak – Figure 7), *A. eburneus* Bogner (Padawan/Penrissen limestones, SW Sarawak – Figure 8), and *A. brachyphyllus* Hett. (Bau limestones, W.Sarawak – Figure 9).

Although limestone aroid floras are indubitably fascinating, and provide much information pertaining to vicariance events and other evolutionary processes, other tropical geologies are as rich, or indeed richer. In recent years, studies focusing on shales and more recently granite have begun to reveal a wealth of geologically endemic taxa.

Figure 3. . *Alocasia reginae* N.E.Br. is another Mulu N.P. endemic, also restricted to limestone, often in swampy forest.

Figure 4. *Alocasia reginula* A.Hay replaces *A. reginae* on the large outcrops of limestone at Bukit Tabin, in eastern Sabah. Unilke *A. reginae, A. reginula* occurs on shaded, dry limestone cliffs.

Figure 5. *Amorphophallus julaihii* Ipor, Tawan & P.C.Boyce occurs in deep holes and among limestone rubble only at Mulu N.P. It is related to several other species in Sarawak.

Figure 6. *Amorphophallus niahensis* P.C.Boyce & Hett. can be thought to 'replace' *A. julaihii* at the Niah Caves, some 130 km west of Mulu.

Figure 7. *Amorphophallus juliae* P.C.Boyce & Hett. is another species related to *A. julaihii*. It is so far known only from a remote forested limestone hill in central Sarawak.

Figure 8. *Amorphophallus eburneus* Bogner was the first species described in the group related to *A. julaihii*. It is only known from the extensive limestone escarpments and stacks of the Penrissen and Padawan ranges in SW Sarawak.

Figure 9. *Amorphophallus brachyphyllus* Hett. occurs on the limestones in the Bau district of western Sarawak. Although the Bau series is but a few kilometres distant from the Padawan series (on which *A. eburneus* occurs) the species never occur intermixed.

Figure 10. *Piptospatha elongata* (Engl.) N.E.Br. is a beautiful aroid occurring only on the granites of NW Sarawak, notably in the Gunung Gading N.P.

Granite provides a difficult habitat for aroids species because it is both acidic and intrinsically impermeable to moisture, so that run-off in periods of heavy rain is intense and strips away much in the way of nutrients and soil cover. Conversely, in periods of dry weather, granite can become very dry and where exposed, very hot. Given these factors, it is little surprise that granite obligated species (e.g., *Piptospatha elongata* (Engl.) N.E.Br. – Figure 10) and *Schismatoglottis liniae* S.Y.Wong & P.C.Boyce (Figure 11) are usually endemic to localized areas, presumably having adapted so far they are 'unable' to leave. However, there may be related species that are equally adapted to particular ecologies. This is indeed the situation with *P. elongata*, for which there are two related, geologically specialized species in the same general area: *Piptospatha impolita* S.Y.Wong, P.C.Boyce & Bogner on hard coastal sandstones (Figure 12), and *P. viridistigma* S.Y.Wong, P.C.Boyce & Bogner on forested limestone (Figure 13).Similarly *S. liniae* is part of a complex of species that are each specialized to particular geologies.

Basalt has much the same suite of ecologies as granite, except that basalts are alkaline. Basalt outcrops are rare in Borneo; although parts of the extensive Ranchan Falls, near Serian, SW Sarwak, and Bukit Quion in Sabah are basalt and both sites feature a number of locally endemic species.

Figure 11. *Schismatoglottis*

Figure 12. *Piptospatha impolita* S.Y.Wong,

Figure 13. *Piptospatha viridistigma* S.Y.Wong,

Figure 14. One of several

liniae S.Y.Wong & P.C.Boyce is another species restricted to granite, also at Gunung Gading.

P.C.Boyce & Bogner occurs on very hard coastal sandstones in NW Sarawak. It is most closely related to granite-obligated *P. elongata* and the limestone-favouring *P. viridistigma*.

P.C.Boyce & Bogner replaces *P. elongata* and *P. impolita* on the heavily forested limestones of western Sarawak.

new *Schismatoglottis* species restricted to shale in Sarawak.

Figure 15. Another as-yet unnamed *Schismatoglottis* from shale geology. It is estimated that fewer than 50% of the *Schismatoglottis* in Borneo have yet been described.

Shales provide an acidic water-permeable habitat which degrades to form very rich soil. Exposed shales in forests tend to be located in isolated patches, and they also tend to be associated with water action which means that shale forests are frequently very 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., of central Sarawak) and thus provide ecological isolation combined with geological specificity. The shales of Borneo harbour by far the largest and most diverse aroid flora on the island. Although studies are still in their early stages it is already clear that a great many of these shale-specialist species are yet to receive even a formal name. Among the wealth of shale-obligated aroid species in Borneo are several remarkable unnamed chasmophytic *Schismatoglottis* species (Figures 14, 15, 16), the Borneo-endemic *Hapaline celtarix* P.C.Boyce (Figure 17), and many species of *Homalomena*, the most species-rich genus of tropical Asian aroids, including *H. striateiopetiolata* P.C.Boyce & S.Y.Wong (Figures 18 & 19), *H. pseudogeniculata* P.C.Boyce & S.Y.Wong (Figures 20 & 21), and *H. symplocarpifolia* P.C.Boyce, S.Y.Wong & Fasih (Figures 22 & 23).

Figure 16. A highly attractive *Schismatoglottis* from vertical, wet shale cliffs in Bintulu.

Figure 17. *Hapaline celtarix* P.C.Boyce is one of two species of this otherwise primarily Thai and Indo-Chinese genus occurring in Borneo. All species except shale-restricted *H. celatrix* are limestone obligated.

Figure 18. *Homalomena striateiopetiolata* P.C.Boyce & S.Y.Wong is a spectacular species recently described from shale river-banks in N Sarawak.

Figure 19. *Homalomena striateiopetiolata* P.C.Boyce & S.Y.Wong is a spectacular species recently described from shale river-banks in N Sarawak.

Figure 20. *Homalomena pseudogeniculata* P.C.Boyce & S.Y.Wong is a widespread species in the Rejang valley of central Sarawak, often occurring on almost perpendicular earth banks comprised of shale-derived soils.

Figure 21. *Homalomena pseudogeniculata* P.C.Boyce & S.Y.Wong is a widespread species in the Rejang valley of central Sarawak, often occurring on almost perpendicular earth banks comprised of shale-derived soils.

Figure 22. *Homalomena symplocarpifolia* P.C.Boyce, S.Y.Wong & Fasih. is so far known only from the type locality along the catchment of the Ai river in central southern Sarawak. It occurs on deep clay soils over shale.

Figure 23. *Homalomena symplocarpifolia* P.C.Boyce, S.Y.Wong & Fasih. is so far known only from the type locality along the catchment of the Ai river in central southern Sarawak. It occurs on deep clay soils over shale.

Unlike Peninsular Malaysia, where granites predominate, Borneo is notable for large tracts of undulating forested sandstone habitats. These are highly diverse in their woody floristic composition, possibly in part because they are subject to marked edaphic differences owing to the ridges and hills coastal *vs* inland orientation leading to ecological differences between the wet coastal exposures and the 'dry' inland exposures, and are also ecologically discontinuous, such that even adjacent hill systems can be remarkably variable in their general composition. Three examples of ecological differences on sandstones leading to localized speciation are the Penrissen, Matang, Bako, and Santubong sandstones of western Sarawak. In total, together these extend no more than 100 km end to end, yet encompass three distinct sandstone geologies, as well as being separated from one another spatially. The Penrissen and Santubong series, while not related geologically, are very similar in their geomorphology, both being composed of very fine grained and extremely hard sandstones. By comparison, the Matang series (including the Matang massif, and Mts Singgai, and Berendang, and across the Sarawak river the lower flanks of the granite pluton called Bukit Muan (also called Bukit Peninjau) are constructed of large grains and are for the most part soft sandstones. Bako falls somewhere in the middle of these between the hardness of the Matang series and the superhard sandstones of Penrissen.

The Penrissen ranges harbour species, many endemic, which appear very closely related to taxa that are limestone obligated, suggesting that the Penrissen geology provides a habitat, in terms of edaphic conditions, that closely resembles that provided by limestones – a geology also abundant in the Penrissen area. Most striking among the Penrissen aroids is the abundance of *Bucephalandra motleyana* Schott (Figures 24 & 25), a species that while not restricted to limestone elsewhere in Borneo most certainly favours it over other substrates. The genus *Bucephalandra* is absent from Matang, Santubong, and Bako.

Figure 24. *Bucephalandra motleyana* Schott is a rheophyte most often favouring limestone stream beds and banks. However, it can also occur on very hard fine-grained sandstones, as in the Penrissen range of SW Sarawak.

Figure 25. *Bucephalandra motleyana* Schott is a rheophyte most often favouring limestone stream beds and banks. However, it can also occur on very hard fine-grained sandstones, as in the Penrissen range of SW Sarawak.

Figure 26. *Aridarum nicolsonii* Bogner is restricted to river systems on Santubong and the wetter parts of Bako N.P.

Figure 27. *Aridarum nicolsonii* Bogner is restricted to river systems on Santubong and the wetter parts of Bako N.P.

Figure 28. *Aridarum borneense* (M.Hotta) Bogner & A.Hay is from Matang, where it occurs on sandstones and granitidolite waterfalls.

Figure 29. *Ooia grabowskii* (Engl.) S.Y.Wong & P.C.Boyce, a widespread and somewhat variable species in Borneo. It is common on the Matang massif and adjacent sandstones, and also on the Penrissen range, but is absent from Santubong and Bako.

The Santubong sandstones, while of similar hardness to those of Penrissen, support forests (and aroid species) quite different to those of Penrissen and in fact show more similarity to the aroid flora of the Matang series. For example *Aridarum*, a genus absent from Penrissen, is abundantly represented on Santubong by *A. nicolsonii* Bogner (Figures 26 & 27) but at Matang this is 'replaced' by *A. borneense* (M.Hotta) Bogner & A.Hay (Figure 28). Another reason for the strong floristic contrast between Penrissen and Santubong may be that Penrissen receives three times more rain per annum (up to 7 m per annum) than Santubong.

The Matang series are also very wet (with up 5 m rain *per annum*) but unlike the Penrissen range the sandstones are highly water-permeable. Matang and Penrissen both support dense mixed lowland dipterocarp forest with a high canopy (40 m), and both have a very rich riverine flora, with some species showing commonality, e.g., *Ooia grabowskii* (Engl.) S.Y.Wong & P.C.Boyce (Figure 29). The Penrissen range, being higher (max 1250 m) than Matang (max 910 m) is also home to extensive oak-laurel-chestnut forests above 900 m. Matang has a comprehensive flora of endemic aroids. Several species of *Schismatoglottis* (e.g., *S. mayoana* Bogner & M.Hotta (Figure 30) and *S. matangae* S.Y.Wong – Figure 31) and *S. matangae,* one of several often locally-restricted related species notable for having leaves that are strongly aromatic when crushed. Other species of the group occur on limestone, granites (i.e., *S. liniae* at Gunung Gading), and shales. Also from Matang is recently described *Homalomena debilicrista* Y.C.Hoe, S.Y.Wong & P.C.Boyce (Figure 32), which is endemic to one small area of the Matang massif and occurs sympatrically with another novel, as yet undescribed species (Figure 33).

Figure 30. *Schismatoglottis mayoana* Bogner & M.Hotta is one of many aroids that are restricted to the Matang system. It occurs along the edges of waterfalls (but not in the waterflow) on vertical soft sandstones.

Figure 31. *Schismatoglottis matangae* S.Y.Wong is another Matang endemic. One of several locally restricted and related species notable for having leaves aromatic when crushed. Other species occur on limestone, granites (i.e., *S. liniae* at Gunung Gading), and shales.

Figure 32. *Homalomena debilicrista* Y.C.Hoe, S.Y.Wong & P.C.Boyce is a recently described species that is endemic to one small area of the Matang massif. It occurs sympatrically with another novel, as yet undescribed species (see Fig. 33).

Figure 33. The second, still undescribed species that occurs sympatrically with *H. debilicrista* at Matang.

Figure 34. *Schismatoglottis nicolsonii* A.Hay may be thought of as the counterpart of the Matang *S. mayoana*. It, too, occurs on vertical sandstone surfaces close to waterfalls.

Figure 35. A new *Homalomena* so far found only at Bako N.P.

Figure 36. *Homalomena havilandii* Ridl. is a highly distinctive species that occurs in large stands at Bako but which is absent from Santubong.

Figure 37. *Bakoa lucens* (Bogner) P.C.Boyce & S.Y.Wong was recently recognised as a new genus endemic to Bako, where it occurs on exposed sandstone boulders in fast-moving streams.

Figure 38. *Bakoa lucens* (Bogner) P.C.Boyce & S.Y.Wong was recently recognised as a new genus endemic to Bako, where it occurs on exposed sandstone boulders in fast-moving streams.

Figure 39. An undescribed rheophytic *Homalomena* that is restricted to Bako.

Canopy heights at Santubong, and especially Bako, are much lower than at Matang, and the riverine floras notably poorer, although with no shortage of endemics such as *Schismatoglottis nicolsonii* A.Hay (Figure 34) and an undescribed *Homalomena* at Bako (Figure 35). *Schismatoglottis nicolsonii* may be thought of as the counterpart of the Matang *S. mayonana*. It, too, occurs on vertical sandstone surfaces close to waterfalls, although occasionally it is also found on the flanks of the small bornhardts (dome-shaped, steep-sided, bald rock outcroppings) that are a feature of the Santubong peninsula.

On its coastal side Bako receives somewhat more rain than does Santubong, but the land side is much drier. Furthermore, because it is not a very high mountain Bako seems less able to facilitate storm clouds forming directly above it and this may account for the marked floristic differences between Bako and Santubong. These semi-different edaphic conditions are in part reflected at Bako by the presence of aroid species in common with Santubong (e.g., *Aridarum nicolsonii*) but in addition species that are absent from Santubong (e.g., *Homalomena havilandii* Ridl. - Figure 36) or even unique to Bako, such as *Bakoa lucens* (Bogner) P.C.Boyce & S.Y.Wong (Figures 37 & 38), and an as yet undescribed rheophytic *Homalomena* (Figures 39 & 40).

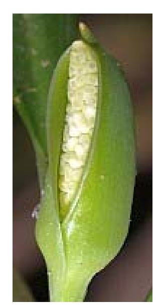

Figure 40. An undescribed rheophytic *Homalomena* that is restricted to Bao.

The above brief piece is only intended to present the barest overview of the extraordinary aroid flora of Borneo, and give indications of habitats where the rocks appear to play a role in defining the plants occurring upon them.

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