The Araceae of Borneo–The Genera

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ABSTRACT

A summary of the aroids of Borneo of the rank of genus and above is offered. 36 genera are listed, of which 35 are indigenous, and one (*Typhonium* Schott) genuinely naturalized. Of the 35 indigenous genera, eight (*Aridarum* Ridl., *Bakoa* P.C.Boyce & S.Y.Wong, *Bucephalandra* Schott, *Ooia* S.Y.Wong & P.C.Boyce, *Pedicellarum* M.Hotta, *Phymatarum* M.Hotta, *Pichinia* S.Y.Wong & P.C.Boyce, and *Schottariella* P.C.Boyce & S.Y.Wong) are Bornean endemics. Four additional genera (*Caladium* Vent., *Dieffenbachia* Schott, *Syngonium* Schott, and *Xanthosoma* Schott) are listed as adventives. The aroid flora of Borneo currently stands at 670 indigenous species, of which more than 40% are undescribed novelties, and with this figure based significantly on our understanding of the flora of Sarawak, Sabah and Brunei (i.e. less than one third of the total landmass). Kalimantan, comprising more than 70% of the land area of Borneo remains very poorly known, and undoubtedly harbors a great many novel species. It is estimated that the total aroid flora for Borneo quite likely exceeds 1,000 species, with barely one third of these described. Borneo is an aroid habitat of global significance, and arguably one of the richest and diverse on the planet. World and Bornean taxonomy and ecology are briefly outlined, along with a summary of the history of aroid fieldwork in Borneo. The most recent key literature is cited, and keys to Bornean aroid taxa of genus and above are presented. Most genera are illustrated.

PREAMBLE

The aroid flora of Borneo is one of the richest on the planet, comprising at least 670 species (Boyce, Croat & Wong, unpub. data), of which approximately 40% remain to be described. Remarkably, these data are based significantly on our understanding of the flora of Sarawak, Sabah and Brunei (i.e. less than one third of the total landmass). Kalimantan, comprising more than 70% of the land area of Borneo, remains very poorly known, and undoubtedly harbors a great many novel species. We estimate that the total aroid flora for Borneo quite

likely exceeds 1,000 species, with barely one third of these described. In short, Borneo is an aroid habitat of global significance, and arguably one of the richest and most diverse on the planet.

HISTORY OF AROID RESEARCH FIELDWORK IN BORNEO

Over the past almost two centuries Borneo has been witness to numerous expeditions which undertook significant sampling of biodiversity, as well as many specifically plant-related excursions, usually by individuals. Thus our knowledge of the aroids of Borneo, such as it is, is based in part on data and samples gathered by field naturalists with varying levels of interest in the family.

Among the earliest collecting in Borneo pertinent to aroids was that by the Dutch botanist Pieter Willem Korthals (1807–1892). Korthals arrived at Banjarmasin, in what is now South Eastern Kalimantan Selatan in late July 1836, and explored the region until mid-December of the same year. His collections were deposited in the Leiden Herbarium, Netherlands, with incomplete sets sent to Buitenzorg Herbarium (now Herbarium Bogoriense) in Java, and to various herbaria in Europe.

Next on the scene was Yorkshireman James Motley (1822–1859) who went to Labuan (an island in the Bay of Brunei, between modern Brunei and the Malaysian state of Sabah) in 1849 to pioneer coal mining and other enterprises for the Eastern Archipelago Company. Although Motley did not have a good relationship with Hugh Low, the other naturalist in Labuan at the time, he corresponded with numerous botanists, especially William Jackson Hooker at Kew Gardens and notably Heinrich Wilhelm Schott in Vienna. After Motley quit the Eastern Archipelago Company in 1853 he spent time on Singapore and in exploring the coast of Sumatera, before being employed as superintendent of the private Julia Hermina coal mine at Bangkal south-east of Banjarmasin. From here he continued to send plant material, including living aroids, to Europe until he and his family were murdered during a local uprising at the start of the Bandjermasin War.

Englishman Hugh Low (later Sir Hugh Low) came from a significant family of nurserymen in Clapton, north London, and initially arrived in Sarawak, Borneo in early 1845 on a commission from the Honorable East Indian Company, soon resigned and became secretary to James Brooke (the first of Sarawak's 'White Rajahs'). He later explored the Sarawak river and many of its tributaries before traveling to Labuan in modern-day Sabah, where he was to be based from 1848–1877, and from where he made many excursions, including the first European ascent of Mt. Kinabalu. Although Low's main interest was orchids, during his travels he collected numerous aroids, many of which he shipped living to the family company in England.

In terms of land area covered the most extensive explorations ever of Borneo remain those of Anton Willem Nieuwenhuis (1864–1953), a surgeon in the Dutch East Indian Army, and later Prof. of Ethnology of the Dutch East Indies. Nieuwenhuis traveled extensively through what is now Kalimantan between 1896 and 1934. His expeditions are especially notable for the quantity of living plants, collected mainly by his European assistants, particularly Johann ('Hans') Gottfried Hallier (1868–1932) and later Gustaaf Adolf Frederik Molengraaf (1860–1942), and Indonesian *mantris*, and sent to Buitenzorg (Bogor) Botanical Gardens, Java, to be cultivated. These living collections significantly assisted Alderwerelt and Engler in their studies. Nieuiwenhuis' herbarium collections were deposited in Bogor and Leiden.

Despite the preceding activities, it can still be fairly said that the history of intensive systematic aroid research in Borneo begins with the extraordinary activities of Italian naturalist Odorado Beccari (1843–1920). While best remembered for his work on palms (Arecaceae), a group in which he specialized throughout most of his adult life, through his prodigious collecting activities, Beccari made significant contri-

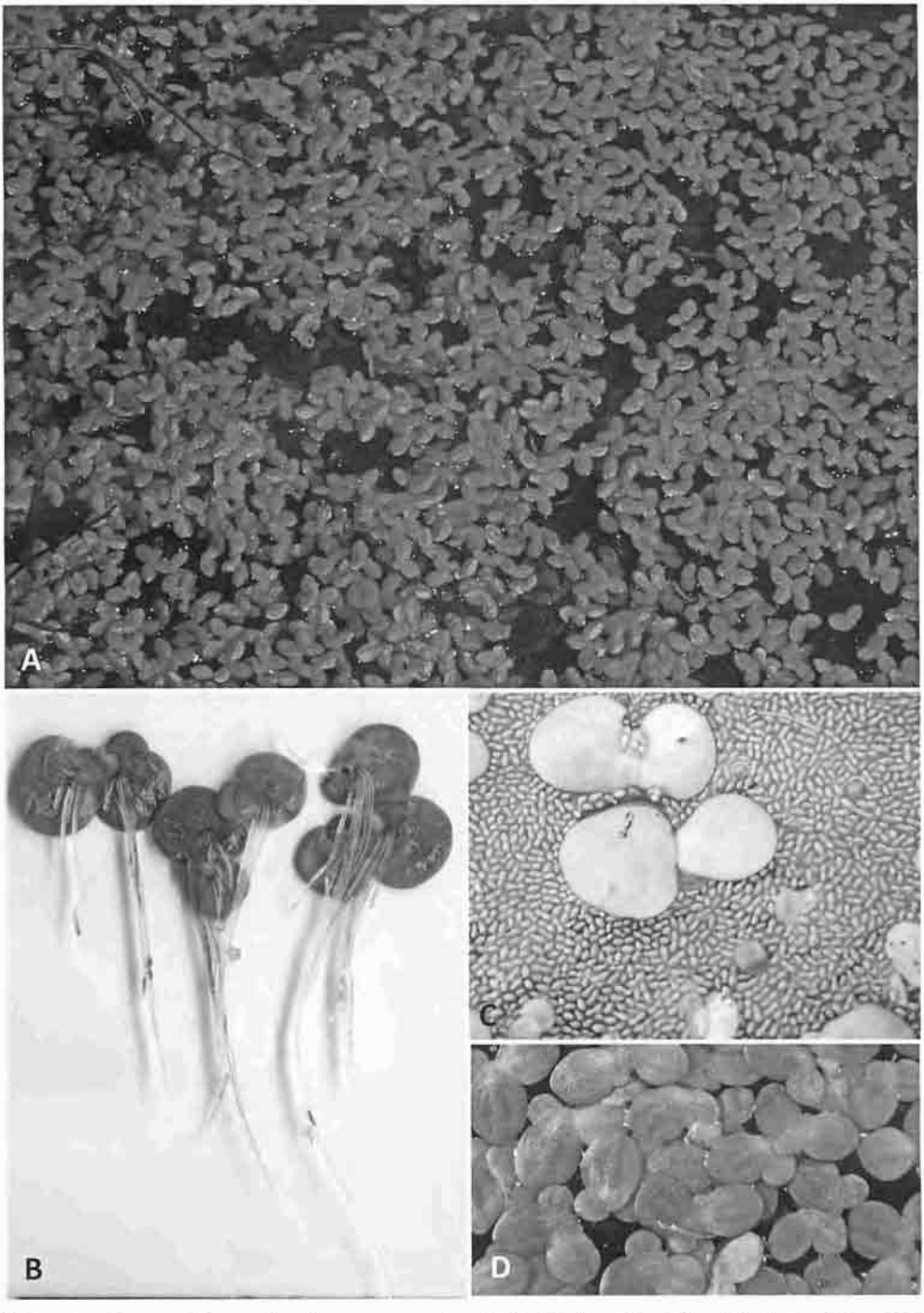

Plate 1. **Lemnoideae. A.** *Lemna aequinoctialis* Welw. **B.** *Spirodela polyrrhiza* (L.) Schleid. Note the multiple roots emerging from each plant body and the reddish coloration. **C.** Minute *Wolffia globosa* (Roxb.) Hartog & Plas surrounding *Spirodela polyrrhiza*. **D.** *Lemna minor* L.

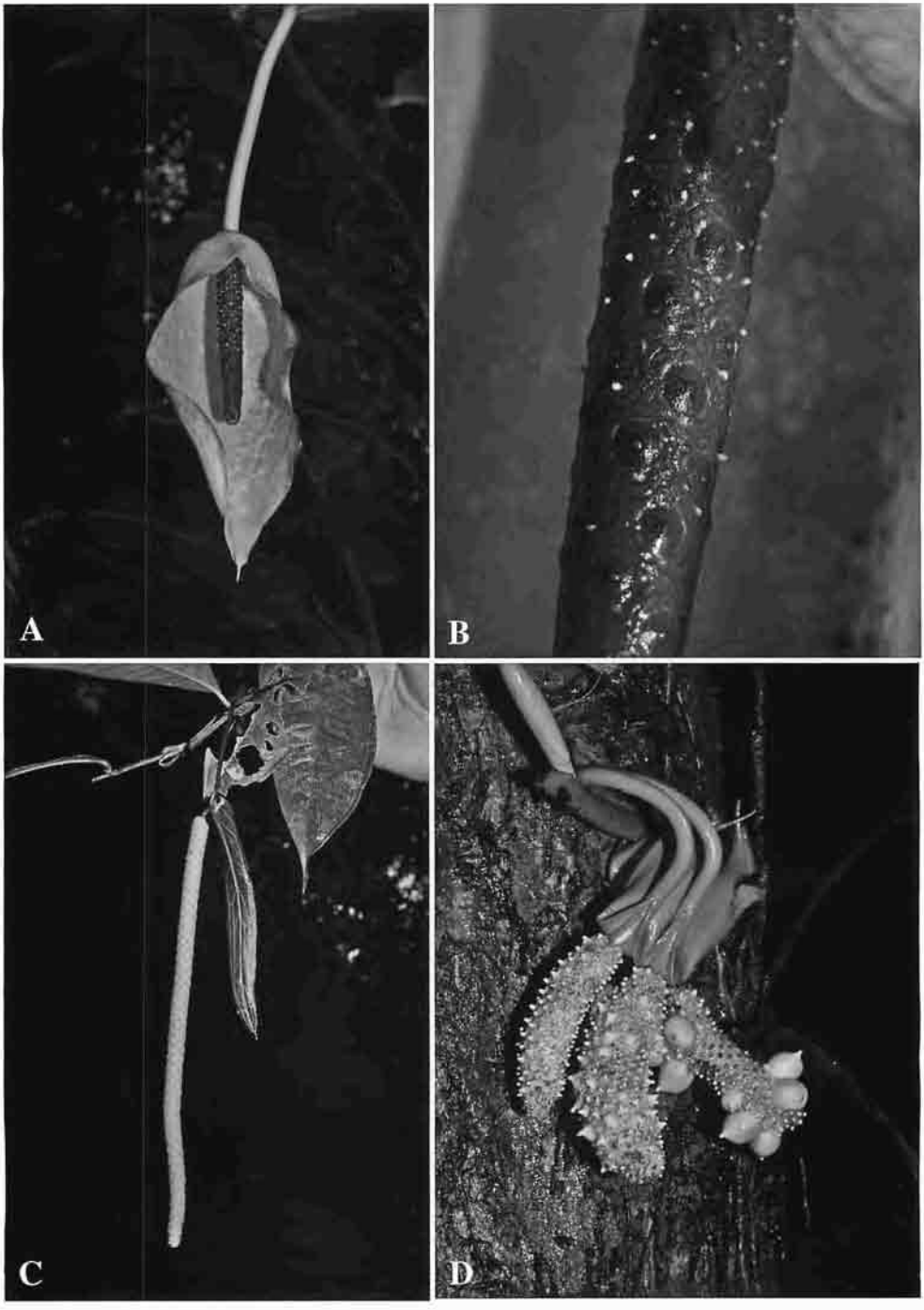

Plate 2. **Potheae: *Pothos* L. A** & **B:** *Pothos atropurpurascens* M.Hotta. A: Note the diagnostic large, inflated, lavender spathes. **B.** Spadix details with the tepals clearly visible around each flower. **C:** *Pothos mirabilis* Merr. **C.** Freshly opened inflorescence. Over the next few days the spadix will extend to double the pictured length. **D:** *Pothos insignis* Engl.

butions to numerous other plant families, in particular the aroids (Araceae), for which family he is famous for introducing to Europe the Titan Arum (*Amorphophallus titanum* (Becc.) Becc.) from Sumatera in 1878. The imagination-capturing nature of this indisputably remarkable plant has, somewhat regrettably, overshadowed Beccari's exemplary aroid work in Sarawak, when through general collecting from 1865–1868 he made the first significant gatherings of the extraordinarily rich aroid flora of N.W. Borneo at a time when virtually every aroid he touched was new to science.

The bulk of Beccari's Bornean aroid material was worked up by Engler, primarily in the *Bullettino della Reale Società Toscana di Orticultura* (Engler, 1879a), the *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* (Engler, 1881), and in Beccari's *Malesia* (Engler, 1883), with additional taxa and notes appearing in *Monographiae Phanerogamarum* (Engler, 1879b), and *Das Pflanzenreich* (Engler, 1912). Beccari himself wrote up several aroid species (Beccari, 1879, 1882). Later research (predominantly based on Beccari's extensive New Guinea collections) revealed novel *Cyrtosperma* Griff. species (Hay, 1988), while a remarkably high percentage of the Bornean *Cryptocoryne* Fisch. ex Wydler are based on Beccari types (see Jacobsen, 1985).

Beccari was notable for the prolonged time spent in Sarawak studying its natural history, and in that respect alone was a remarkable man. However, no less remarkable were those Europeans sent out by their respective governments as administrators, and who would often spend years living in government stations in remote headwaters, dividing their time between administering the often enormous areas under their jurisdiction and exploring the abundant wildlife. Charles Hose, sent to Sarawak as a trainee cadet under the Rajah Sir Charles Brook, arrived in Sarawak in 1884 and was in 1888 stationed in Baram, in the even now remote N.E. of the state. Hose was eventually to spend over 25 years in Sarawak, of which 20 years was spent in Baram. Among Hose's remarkable feats were the exploration of the Hose Mountains, the range that separates the valleys of the Rejang and Baram rivers, and the first extensive exploration of the limestone systems of Niah, among much else. Although not specifically an aroid collector, the very nature of Hose's fieldwork in botanically unexplored areas netted many novel collections. These were later worked up by Rendle (1901).

The next person to visit Borneo, specifically Sarawak, with a particular interest in aroids was Henry Nicholas Ridley (1855–1956). Ridley, a prodigiously productive botanist, made a series of visits to Borneo between 1893 and 1915 and through the resulting publications (in particular Ridley, 1902, 1905, & 1913) established a framework of Borneo-specific knowledge that forms the basis for much of the aroid research to this day.

After serving in the DEI Army until pensioned through deafness, Cornelis Rugier Willem Karel van Alderwerelt van Rosenburgh (1863–1936) was based in Bogor (then Buitenzorg) Herbarium initially as a Temporary Assistant of the Herbarium (1905–1908), then as Conservator, and later Acting Assistant (1910–1922). Although principally interested in ferns, Alderwerelt produced three important papers cataloging and describing living aroids in the gardens, many of which originated

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Most *Pothos* produce fruit ripening red or dark orange. Different populations of *Pothos insignis* have fruits ripening white (as here), purple, white with a purple top, and pale orange. It is not yet clear whether these populations deserve taxonomic recognition.

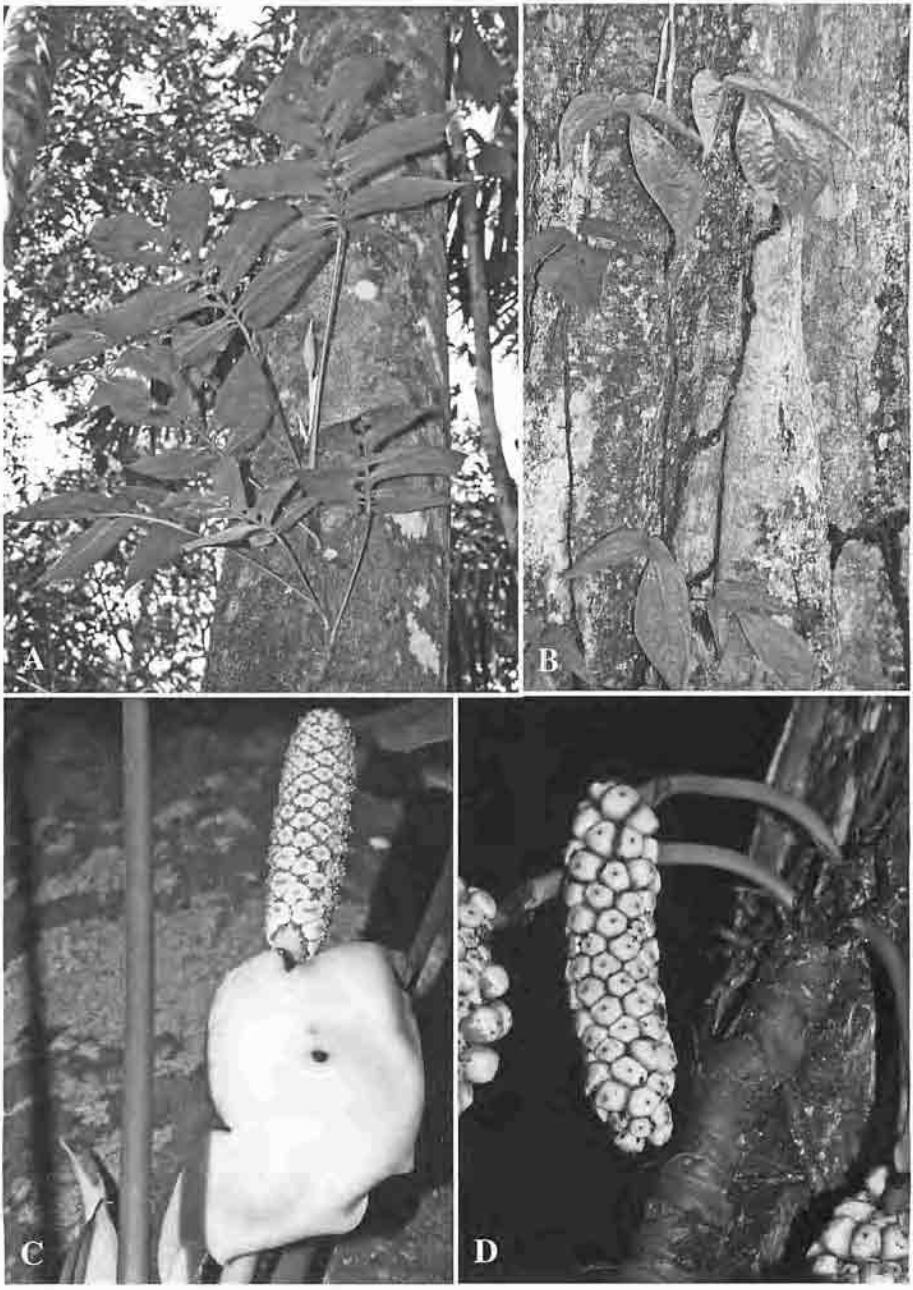

Plate 3. **Monstereae: *Amydrium* Schott. A–D:** *Amydrium medium* (Zoll. & Moritzi) Nicolson. *Amydrium medium* is unusual among hemiepiphytic monsteroids in remaining small, usually climbing less than 4 m, and thus flowering low on the tree trunk. Adult plants have the leaves both perforated and pinnately divided (**A**). Juvenile plants have less elaborately divided leaves (**B**). As in most Monstereae the spathe is shed during anthesis (**C**), but unlike most the fruits are indehiscent berries (**D**).

from Nieuwenhuis' Borneo expeditions (see above), and fieldwork in Sumatera. Alderwerelt did very little fieldwork, and as far as is known never visited Borneo, and there has been a tendency to regard Alderwerelt's aroid publications as amateur 'tampering', especially since the first paper in the series is somewhat intemperately critical of Engler's then just-completed and magisterial species-level *Das Pflanzenreich* account. However, while Alderwerelt did undoubtedly over-describe some species, much in the same way as did Furtado, and his work based on herbarium specimens alone leaves rather much to be desired, there is little doubt that much of his work based on the living plants with which he was familiar, and of which he made excellent observations, is of the first order. Given the then very poor state of knowledge of the aroids of Borneo, and also Sumatera, another island then well-represented in the Garden's collection, Alderwerelt's aroid publications (Alderewelt, 1920, 1922a, 1922b) remain a milestone in our increased understanding of Sundaic aroids.

After Ridley and Alderewerelt, and notwithstanding that Caetano Xavier Dos Remedios Furtado (1897–1980) remained active in Singapore and Peninsular Malaysia through much of the 1930s and via his publications impacted to some extent on the flora of Borneo (notably Furtado, 1939), there was a hiatus of field-based activity in Borneo until American Dan H. Nicolson undertook extensive aroid collections through the region during the early 1960s. These studies, in part for his doctoral work on *Aglaonema* Schott (Nicolson, 1964, 1969), also produced revisions of *Amydrium* (Nicolson, 1968c), Asian *Spathiphyllum* (Nicolson, 1968b), and then generic *Xenophya* (Nicolson, 1968a). At roughly the same time Japanese Botanist Mitsuru Hotta began fieldwork in Sarawak and Brunei, concentrating especially on *Schismatoglottis* and its allies (Hotta, 1965, 1966a, 1966b, 1967, 1976), and within a few years Josef Bogner and Niels Jacobsen began their still ongoing work on the Schismatoglottideae and *Cryptocoryne* (e.g. Bogner, 1979, 1980, 1981, 1983a, 1983b, 1983c, 1984a, 1984b, 1988, 1989; Bogner & Hotta, 1983a, 1983b; Jacobsen, 1985).

In the past 25 years several other botanists have entered the Borneo aroid arena, beginning with Alistair Hay in the early 1980s and Peter Boyce in the mid 1980s. Hay began by tackling the lasioids as part of his doctoral research, and then went on to study and monograph *Alocasia* (Hay, 1998, 2000), *Colocasia* (Hay, 1996), *Schismatoglottis* (Hay & Yuzammi, 2000; Hay, 2002; Hay & Herscovitch, 2003), contributed significantly to studies of *Pothos* (Boyce & Hay, 2001), the Schismatoglottideae (Bogner & Hay, 2000), and *Homalomena* (Hay & Herscovitch, 2002), complied an enormously useful checklist and bibliography for Malesian aroids (Hay *et al.*, 1995), and also co-authored the remarkable discovery of hitherto West African endemic *Nephthytis* Schott in Sarawak (Hay, Bogner & Boyce, 1994).

Peter Boyce, while based at Kew Gardens, undertook numerous visits to research and monograph hemiepiphytic aroids in Sunda. He eventually settled permanently in Sarawak in the early 2000s and has since concentrated among other things on the mesophytic aroids of Sarawak (e.g. Bogner & Boyce, 2009; Boyce, 1994, 1996, 1998, 2001, 2005, 2006a, 2006b, 2007; Boyce, Jeland & Jipom, 2005; Boyce, & Poulsen, 1994; Boyce & Wong, 2008a, 2008b, 2009).

Japanese botanists Hiroshi Okada and Yasuko Mori are now working in Kalimantan, particularly on Schismatoglotideae (Okada, 2000; Okada & Mori, 2000; Okada, Tsukaya & Mori, 1999), while Malaysian, Indonesian, Japanese and Dutch plant enthusiasts such as Isa b. Ipor, Hendra Budianto, Suwidji Wongso, Hiroyuki Kishi, Takashige Idei, Yuji Sasaki, and Jan Bastmeijer are singly and in collaboration generating excellent outputs on *Cryptocoryne* (Bastmeijer, 2002; Budianto & Basjmeijer, 2004; Ipor, Tawan & Jacobsen, 2005, 2006; Ipor *et al.*, 2007a, 2007b, 2008a, 2008b; Jacobsen, 2002; Jacobsen, Bastmeijer & Sasaki, 2002; Sasaki, 2002; Wongso & Bastmeijer, 2005). Isa b. Ipor has also an

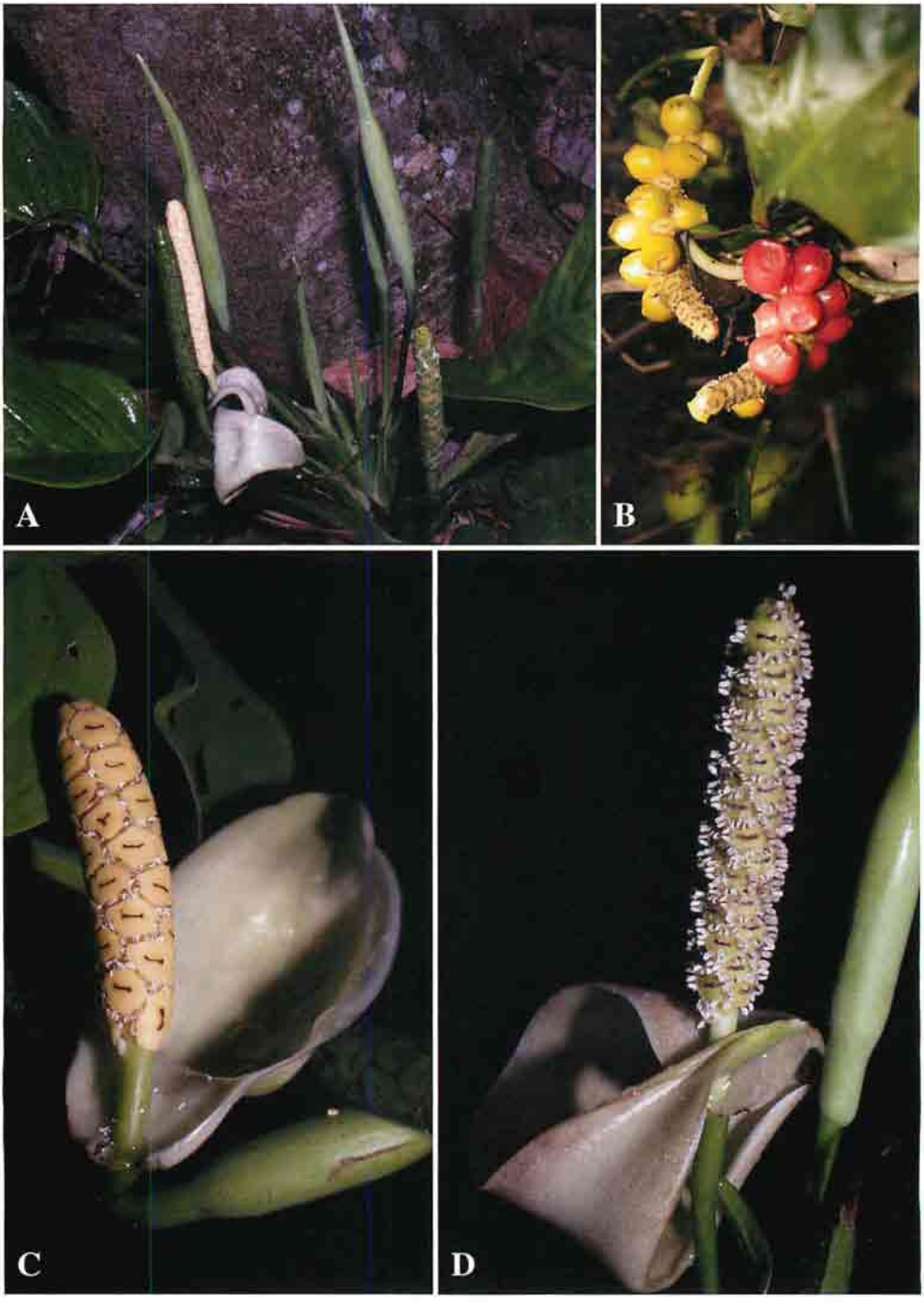

Plate 4. **Monstereae: *Anadendrum* Schott. A.** *Anadendrum calcicola* P.C.Boyce, Ipor & S.Y.Wong, a recently described species restricted to karst limestone towers in Sarawak. Note the bi-modular fan-shaped arrangement of the inflorescences, with the inflorescences developing sequentially and alternately from one axis to another. Note also the distinctly

interest in *Amorphophallus* (Ipor, Tawan & Boyce, 2004).

Most recently Sarawakian Wong Sin Yeng has begun undertaking the first critical study of evolution and taxagenesis in Sundaic aroids using a combination of extensive fieldwork and molecular analyses. Her data are already changing generic frameworks and forcing re-examination of our understanding of the aroids of Borneo (Boyce & Wong, 2006, 2007, 2008c; Wong & Boyce, 2007a, 2007b, 2008; Wong, Boyce & Bogner, 2009; Wong *et al.*, 2010).

KEY TO THE SUBFAMILIES AND TRIBES OF BORNEAN ARACEAE

1a. Plants comprising small to minute few-rooted or rootless free-floating thallus-like leafless bodies . . . . . **Lemnoideae**

1b. Plants not as above. If free-floating then leaves forming a conspicuous rosette with copious roots hanging beneath

2a. Flowers bisexual each with a perigone of conspicuous tepals

3a. Armored helophytes with hastate to 4×pinnatifid leaves . . . . **Lasioideae**

3b. Climbing hemiepiphytes with (mostly) elliptic leaves . . . . . **Pothoideae**

2b. Flowers bisexual without a perigone of conspicuous tepals, or unisexual

4a. Flowers bisexual, perigone if present membranous and inconspicuous; mainly climbing hemiepiphytes, rarely rheophytic . . . . . **Monsteroideae**

4b. Flowers unisexual

5a. Free-floating plants with leaves forming a conspicuous rosette with copious roots hanging beneath . . . . . **Aroideae: Pistieae**

5b. Not so

6a. Leaves

7a. Leaves decompound. Inflorescences appearing before leaf emergence, with flowers of both sexes . . . . . **Aroideae: Thomsonieae**

7b. Leaves trifoliolate to pentafoliolate. Inflorescences produced with leaves, single-sexed . . . . . **Aroideae: Arisaemateae**

6b. Leaves simple, ranging from linear-lanceolate to hastate

8a. Aquatic plants. Infructescences composed of dehiscent carpels . . . . . **Aroideae: Cryptocoryneae**

8b. Plants not aquatic. Infructescences comprised of berries.

9a. Plants suffruticose. Fruits conspicuous red or pink berries not surrounded by a persistent spathe . . . . . **Aroideae: Aglaonemateae**

9b. Plants not suffruticose. Fruits various, if red or orange red berries then surrounded by a persistent spathe

10a. Entire spathe closing after anthesis and then persisting until fruit maturity

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long-beaked spathe prior to opening. **B.** *Anadendrum muluensis* P.C.Boyce, Ipor & S.Y.Wong, showing the distinctive truncate-topped fruits with a transverse stigma. The upper left infructescence is unripe. **C.** *Anadendrum muluensis*, is unusual in the genus in the anthers not exserting by filament extension during male anthesis. Instead the anthers release their pollen while still submerged between the gynoecia. **D.** An undescribed *Anadendrum* from Gunung Gading N.P., NW Sarawak. Here the stamens are exserted strongly from between the gynoecia, but uniquely the spathe is pink-tinted.

Plate 5. **Monstereae: *Epipremnum* Schott. A–C.** *Epipremnum pinnatum* (L.) Engl. **A.** Mature plant. **B.** detail of active shoot apex with the conspicuous dense fibrous cataphyll, prophyll and petiolar sheath fiber. **C.** Synflorescence with two developing infructescences and an inflorescence at male anthesis. **D.** Detail of spadix base at late male anthesis. Note the conspicuous exserted stamens and that lowermost flowers produce no stamens. These flowers are functionally sterile (gynoecia also lacking ovules) and are associated with the production of sticky droplets that are likely involved with pollinator reward.

11a. Rhizomatous geophytes. Leaves solitary or rarely 2 together, distant from each other. Inflorescences arising directly from the ground. Spathe forced open by developing fruits but not actively splitting. Fruits a large conspicuous red berry containing a large solitary green seed . . . . . **Aroideae: Nephthytideae**

11b. Clumping mesophytes. Leaves many together. Inflorescences arising from leafy shoots. Spathe actively splitting from the base and peeling upwards to reveal fruits. Fruits many, whitish to very pale pink, each containing many tiny brown or black seeds . . . . . **Aroideae: Homalomeneae**

10b. Upper spathe mostly shedding during or soon after anthesis, and lower spathe persisting until fruit maturity; if upper spathe persisting then attached portion of petiolar sheath very short and the remainder free-ligular ***or*** absent and the protective role taken on by prophyll/cataphyll

12a. Staminate flowers forming synandria

13a. Spathe not obviously with a lower tubular part separated from the spathe limb by a conspicuous constriction. Pistillate flowers very few, arranged in a single vertical row. Fruits ripening white, enclosed in the folded lower spathe but ***not*** exposed by the lower spathe actively splitting . . . . . **Aroideae: Caladieae**

13b. Spathe with a well-defined lower tubular part separated from the spathe limb by a pronounced constriction and forming a chamber enclosing all or most of the pistillate flower zone. Pistillate flowers many, arranged in a dense spiral. Fruits ripening red or yellow-brown, exposed by the lower spathe actively splitting . . . . . **Aroideae: Colocasieae**

12b. Staminate flowers not forming synandria

14a. Tuberous-stemmed geophytes. Sterile flowers between the staminate and pistillate flower zones filamentous and tangled. Spadix with a long, naked appendix. . . . . **Aroideae: Areae**

14b. Mesophytes, rheophytes, lithophytes and chasmophytes with stems never tuberous. Sterile flowers between the staminate and pistillate flower zones if present never filamentous and tangled. Spadix appendix, if present, never naked. . . . . **Aroideae: Schismatoglottideae**

Subfamily Lemnoideae

Despite their radically different appearance from the remainder of all other aroids the scientific evidence is now overwhelmingly in support of the inclusion of the duckweeds (formerly family Lemnaceae) in the Araceae, where they appear basal to all bisexual-flowered aroids above Gymnostachydoideae+Orontiodeae (Cabrera *et al.*, 2008). The extremely reduced vegetative form and minute reproductive structures make studying the species a delicate and time-consuming activity, although fortunately the taxonomy of the duckweeds has been extensively and rigorously studied by Landolt (1986). A useful website with numerous excellent images maintained by Wayne Armstrong may be found at www.waynesword.palomar.edu/1wayindx.htm.

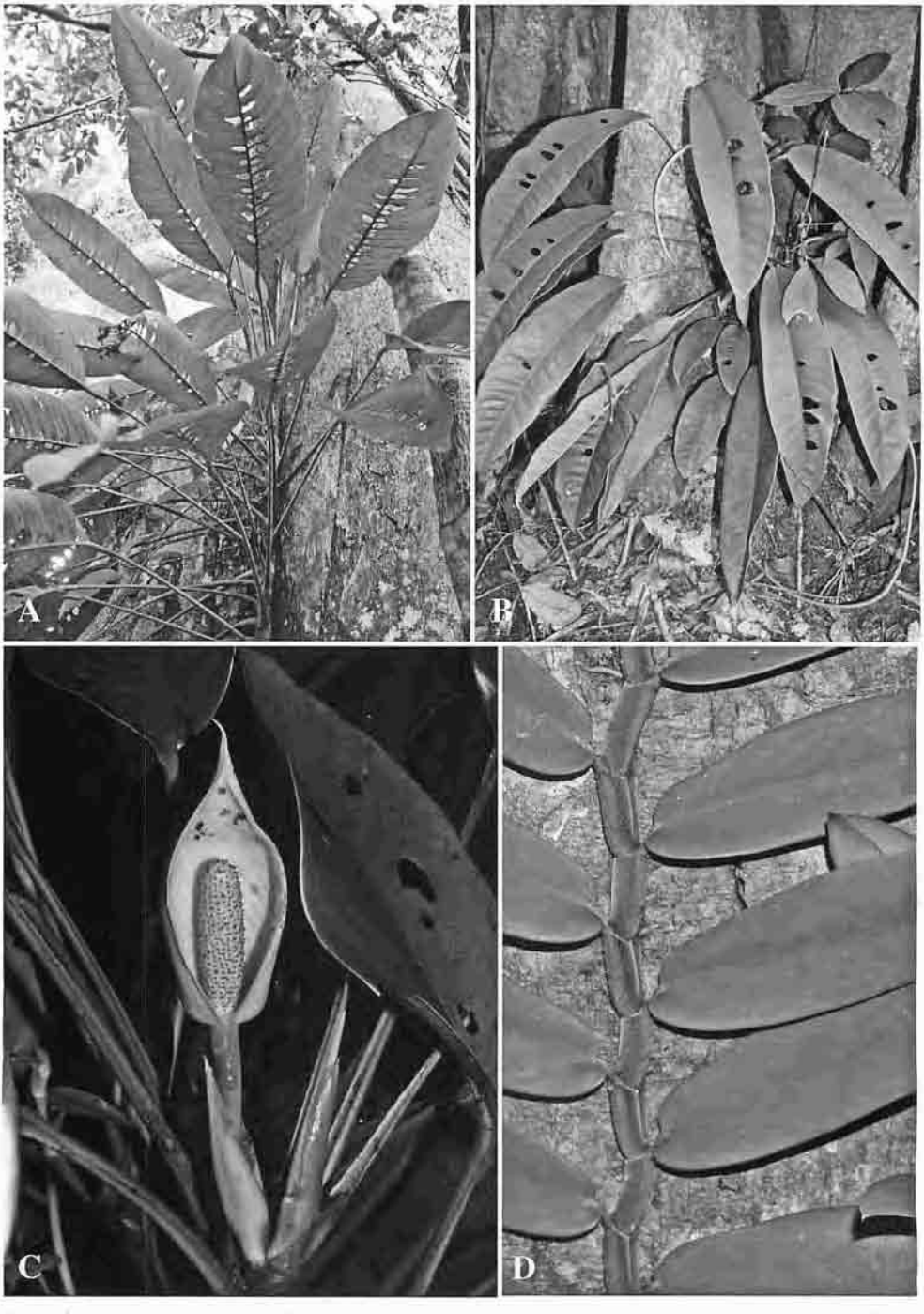

Plate 6. **Monstereae: *Rhaphidophora* Hassk. A.** *Rhaphidophora foraminifera* (Engl.) Engl., a widespread species with, in adult leaves, distinct lines of perforations along either side of the mid-rib. The abaxial surface of the lamina is minutely yellow-pubescent. **B.** *Rhaphidophora megasperma* Engl., although superficially similar to *R. foraminifera*, is in a

Four of the five currently accepted genera of duckweeds occur sporadically in Borneo.

KEY TO THE GENERA OF BORNEAN LEMNOIDEAE

1a. Roots 1–21 per plant body; plant body with 1–21 veins; the daughter plant bodies and inflorescences originating from 2 lateral pouches at the base of the plant body.

2a. Roots (1–) 2–21 per plant body; plant bodies with (3–) 5–21 veins, surrounded at its base by a small scale (prophyll) covering the point of attachment of the roots

3a. Plant bodies 1–1.5 times as long as wide, with 7–12 roots of which 1 (–2) perforate the scale . . . . . ***Spirodela***

3b. Plant bodies 1.5–2 times as long as wide, with (3–) 5–7 veins and (1–) 2–7 (–12) roots all of which perforate the scale . . . . . ***Landoltia***

2b. Roots 1 per plant body; plant bodies with 1–3 veins, without a scale at the base . . . . ***Lemna***

1b. Roots absent; plant body without veins; the daughter plant bodies originating from a single terminal pouch or cavity at the base of the plant body; inflorescence originating in a cavity on the plant body upper surface. . . . . ***Wolffia***

Spirodela Schleid., *Linnaea* 13: 391. 1839; Landolt, *Veröff. Geobot. Inst. ETH, Stiftung Rübel* 71:464. 1986. **Plate 1B, C.**

Small thallus-like floating hydrotherophytes, plant bodies 2 or more together, with 2–12 (or more) roots and 1 (–2) flowers per body.

Taxonomy — World

Three species: one cosmopolitan, one from South America, and one restricted to southern central China.

Taxonomy — Borneo

One species, not endemic.

Ecology

Slow-moving or static water in old monsoon drains and road-side ditches, rare.

Landoltia Les & D.J.Crawford. *Novon* 9: 532. '1999' 2000.

Small thallus-like floating hydrotherophytes, plant bodies 2 or more together, with 2–5 roots and 1 (–2) flowers per body.

Taxonomy — World

One species, widespread in the tropics and subtropics of both hemispheres.

Taxonomy — Borneo

One species, not endemic.

Ecology

Slow-moving or static water in old monsoon drains and road-side ditches, rare.

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different part of the genus, with relationships primarily to Papuasian species. Note that the perforations occur on only one side of the leaf. The abaxial surface is glabrous. **C.** *Rhaphidophora megasperma* inflorescence at late female anthesis. **D.** *Rhaphidophora crassifolia* Hook.*f.* one of the more easily recognizable species of the taxonomically complex Hongkongenenis Group. The stems angular in cross-section and the petiolar sheath reaching the apical pulvinus, and soon falling to leave a scar, are among the diagnostic characters. The majority of species of this group in Borneo have yet to be recognized and formally named.

Plate 7. **Monstereae: *Scindapsus* Schott. A.** Juvenile plant of an undescribed hemiepiphytic lianescent species that reaches 30m+ into the canopy before flowering. **B:** *Scindapsus pictus* Hassk. Juvenile stage of this species, the adult stage comprises of slinging shoots with cordate-based leaves and very long curtains of free shoots with narrow, falcate leaves. **C.** An as yet undescribed epiphytic creeping *Scindapsus* that habitually hosts nests of stinging ants among the roots. **D.** *Scindapsus geniculatus* Engl. Another epiphyte, this forming fans of litter-trapping leaves. Several new species of litter-trapping *Scindapsus* await description.

Notes

Landoltia was separated from *Spirodela* primarily on the basis of molecular studies of the duckweeds aimed at providing additional data for undertaking taxonomic studies in a group with so few macromorphological data. In comparison with *Spirodela*, *Landoltia* plants exhibit a reduction in overall dimensions, number of roots and veins per plant, and have scattered brown epidermal pigment cells (visible on dead plants of *Landoltia punctata*), that are lacking in *Spirodela*.

Lemna L., *Sp. Pl.*: 970. 1753. Landolt, *Veröff. Geobot. Inst. ETH, Stiftung Rübel* 71: 471. 1986. **Plate 1A & D.**

Very small thallus-like floating or slightly submerged hydrotherophytes, plant bodies 2 or more together, with 1 root and 1 (–2) flowers per body.

Taxonomy — World

13 species, widespread in the tropics, subtropics and warm temperate regions of both hemispheres.

Taxonomy — Borneo

Four species, none endemic.

Ecology

Slow-moving or static water in old monsoon drains and road-side ditches, rare except for *L. aequinoctialis*.

Wolffia Horkel ex Schleid. 1844. *Beitr. Bot.* 1: 233. Landolt *Veröff. Geobot. Inst. ETH, Stiftung Rübel* 71: 544. 1986. **Plate 1C.**

Minute rootless thallus-like floating to partially submerged hydrotherophytes; plant bodies solitary or in pairs, more-or-less three-dimensional, with cavities above but without veins or air-spaces; 1 flower per body.

Taxonomy — World

11 species, widespread in the tropics, subtropics and warm temperate regions of both hemispheres.

Taxonomy — Borneo

Four species, none endemic.

Ecology

Slow-moving or static water in old monsoon drains and road-side ditches, rare.

Subfamily Pothoideae
Tribe Potheae

Potheae comprises three genera of forest-dwelling primary hemiepiphytes, *Pothos* L., *Pedicellarum* M.Hotta, and *Pothoidium* Schott, the last absent from Borneo. In Borneo species of tribe Potheae are readily distinguished by their bisexual flowers with a prominent leathery perigone, and infructescences of discrete ellipsoid berries ripening red or orange, very rarely white or purple.

KEY TO THE GENERA OF BORNEAN POTHEAE

1a. Flowers sessile, without a receptacle; tepals of perigone free, very rarely united, if united then not forming a 'cup'. . . . . ***Pothos***

1b. Flowers pedicellate, with a distinct receptacle; tepals of perigone connate, forming a conspicuous 'cup' . . . . . ***Pedicellarum***

Pothos L. Sp. Pl.: 968. 1753; Mayo, Bogner & Boyce, *Genera of Araceae*, 98–99, pl. 5 & 108A, 1997; Boyce & Hay, *Telopea* 9(3): 449–571. 2001. **Plate 2.**

Pothos is divided into two subgenera: *Pothos* and *Allopothos*, with *Allopothos* further divided into two informal supergroups: Allopothos and Goniurus. Subgenus *Pothos* is distinguishable by the lamina-like petiole, lacking an obvious sheath with the whole leaf resembling that of many *Citrus*. Subgenus *Allopothos* has a distinct petiole, sheathing for much of its length. The Allopothos supergroup has a spadix with congested flowers while the flowers of the Goniurus supergroup are scattered, with portions of the spadix axis clearly visible between individual flowers. Species of the Goniurus su-

Plate 8. **Monstereae: *Scindapsus* Schott. A–D:** A small selection from the many undescribed species in the taxonomically complex *S. coriaceus* complex. **A.** Marcescent petiolar sheath and solitary, odorless inflorescences with a marcescent spathe. **B.** Persistent petiolar sheath, and solitary inflorescences smelling strongly of eugenole (clove oil) with

pergroup (notably *P. oliganthus* P.C.Boyce & A.Hay—see Boyce & Hay, 2001) are of interest as they appear to link the genera *Pothos* and *Pedicellarum* (see below).

Taxonomy — World

Approximately 70 species distributed from Madagascar through to India, the subtropical eastern Himalayas, throughout subtropical and tropical Asia into the tropical western Pacific and tropical eastern Australia.

Taxonomy — Borneo

16 species of which 10 endemic.

Ecology

Primary to disturbed secondary lowland to upper hill perhumid evergreen broadleaf subtropical and tropical forest, often on slopes or ridges, less often in poorly drained valley bottoms, at least some species (e.g. *P. insignis* Engl., *P. ovatifolius* Merr., and *P. leptostachyrus* Schott) are limestone obligates.

Pedicellarum M.Hotta *Acta Phytotax. Geobot.* 27: 61 1976; Nicolson, *Aroideana* 7: 56–57. 1984; Mayo, Bogner & Boyce, *Genera of Araceae* 100, pl.6 & 108B. 1997; Boyce & Hay, *Telopea* 9(3): 554–558. 1991.

Despite the paucity of herbarium specimens, and notwithstanding that much material in herbaria previously annotated as *Pedicellarum paiei* M.Hotta is referable to species in the Goniurus supergroup of *Pothos*, suggesting that *Pedicellarum* is a rare species, it is in fact somewhat common and widespread in western Sarawak and neighboring Kalimantan.

Taxonomy — World

One species, endemic on Borneo.

Taxonomy — Borneo

See above.

Ecology

Primary to disturbed secondary lowland to hill perhumid evergreen broadleaf tropical forest, usually on ridges.

Subfamily Monsteroideae

Five Bornean genera are in Monsteroideae: *Amydrium* Schott, *Anadendrum* Schott, *Epipremnum* Schott, *Rhaphidophora* Hassk., & *Scindapsus* Schott. All Bornean Monsteroideae except *Anadendrum* and *Amydrium* are distinguished by a mature infructescence in which the surface is comprised of tough thickened stylar tissue that, when the fruits are ripe, fall as irregular plates to expose the ovary cavity with the seed embedded in copious, variously colored pulp. *Anadendrum* produces infructescences of discrete truncate-topped berries that ripen red or orange, while *Amydrium* in Borneo has rounded berries ripening white. All genera except *Anadendrum* and *Amydrium* have abundant trichosclerieds in all tissues (sparse in *Amydrium*) which are observable by tearing a mature leaf lamina and looking for 'hairs' protruding from the damaged edges.

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the spathe opening widely, and caducous. **C.** Petiolar sheath degrading to fine, tough fibers, with several odorless inflorescences produced sequentially on a specialized leafless shoot, and the caducous spathe barely opening. **D.** Petiolar sheath degrading to wide, weak fibers, with several inflorescences several produced sequentially from the tips of leafy shoots, and smelling weakly of methyl butyrate (pineapple); spathe barely opening, caducous.

Plate 9. **Lasioideae: *Cyrtosperma* Griff. A–D:** *Cyrtosperma ferox* N.E.Br. **A.** Young plant showing the distinctive leaves. **B.** Detail of the petiole bases with their distinctive ascending prickles. **C.** Inflorescence at female anthesis. Note the conspicuous stigma droplets. **D.** Mature infructescence. The nodding posture, marcescent-persistent spathe, and fruits barely emerging from the surrounding tepals are diagnostic in Borneo.

Plate 10. **Lasioideae: *Lasia* Thwaites. A–B:** *Lasia spinosa* (L.) Thwaites. **A.** Flowering plant. Note the greatly attenuated spathe limb opening only at the base. **B.** Ripe infructescence. Note the spinulose berries, **C–E:** *Lasia concinna* Alderw. **C.** Mature leaf with up to 3×pinnation. **D.** Inflorescence at female anthesis. Note that the much shorter spathe opens at the top. **E.** Ripe infructescence. Note the smooth berries.

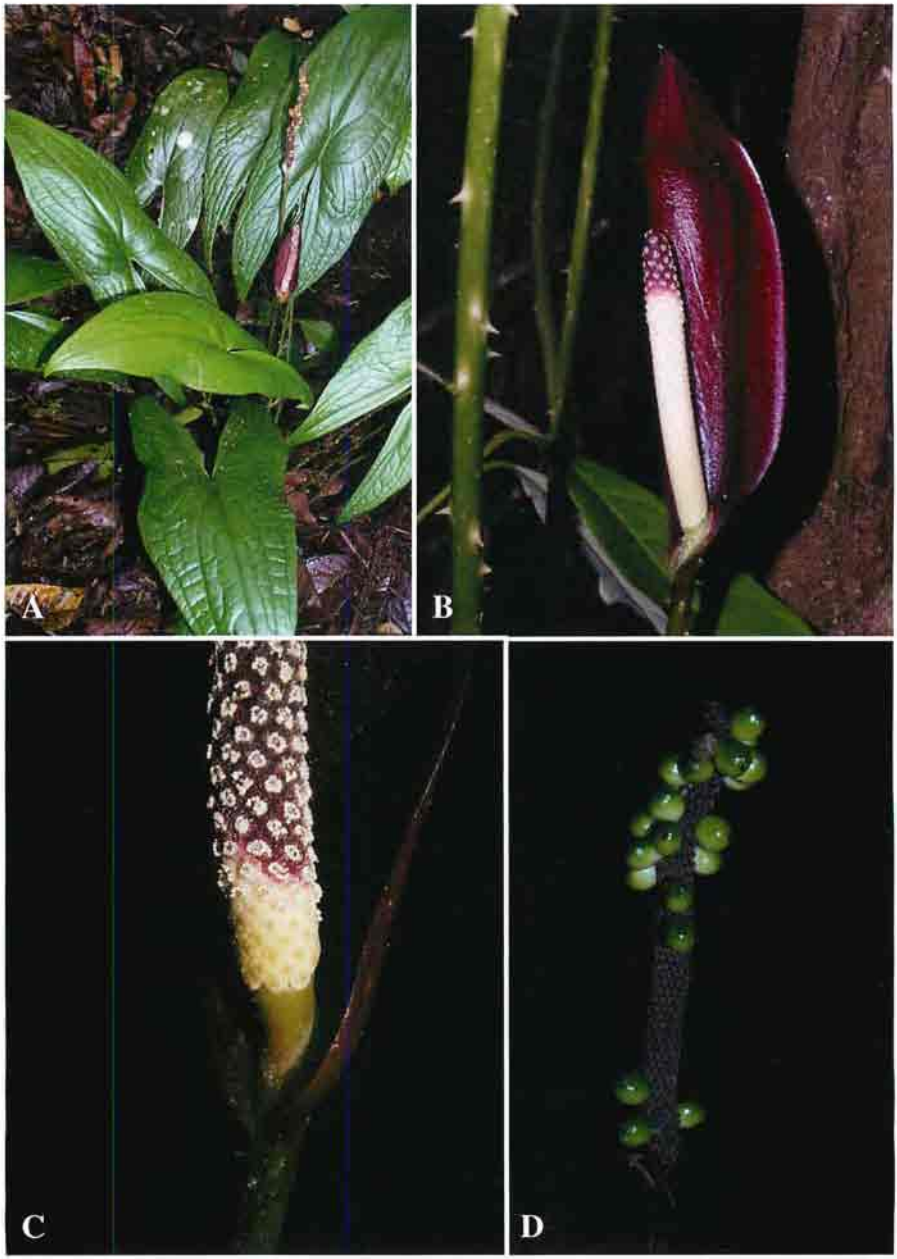

Plate 11. **Lasioideae: *Podolasia* N.E.Br. A–B:** *Podolasia stipitata* N.E.Br. **A.** Flowering and fruiting plant in habitat. **B.** Inflorescence at male anthesis. Note the terminal portion of the spadix is differently colored, this zone comprises flowers that are post anthesis and will proceed down the spadix until post anthesis the entire spadix is purple. **C.** Detail of the spadix base near to completion of anthesis. Note that only a small area of white spadix remains. **D.** Infructescence nearing maturity. Note that the fruits are almost wholly exserted from between the tepals. When ripe the berries are scarlet.

Plate 12. **Aroideae: Homalomeneae: *Homalomena* Cyrtocladon Supergroup. A–F:** *Homalomena banneae* P.C.Boyce, S.Y.Wong & Fasihuddin B.Ahmad. **A.** Flowering plant. **B.** Inflorescence at early anthesis; note the constriction between the lower spathe and limb. The amber-colored resin droplets on the spadix mix with pollen and aid pollen adhesion

KEY TO THE GENERA OF BORNEAN MONSTEROIDEAE

1a. Spathe in bud stout, short- to long-stout-pedunculate, not conspicuously long-beaked, if beak present then less than 1/6 length of entire spathe, opening with inside yellow, orange, greenish or white, only moderately waxy. Flowers naked. Infructescence a monsterocarp or, if with discrete berries, then these not truncate, and ripening white. Trichosclereids present (but sparse in *Amydrium*)
- 2a. Adult leaf leaf pinnate *and* conspicuously perforated. Higher order venation completely reticulate. Infructescence with discrete berries ripening white. Trichosclereids sparse . . . . . ***Amydrium***
- 2b. Trichosclereids abundant (many 'hairs' apparent when a mature leaf lamina is torn). Higher order venation striate or reticulate
  - 3a. Ovules 2–6 or more, placentation parietal. Fruits with more than one seed
    - 4a. Ovules 8 or more, superposed on 2 (rarely 3) parietal placentas. Seeds many, ellipsoid, straight, 1.3–3.2 mm long, 0.6–1 mm wide; testa brittle, smooth . . . . . ***Rhaphidophora***
    - 4b. Ovules 2–4 (–6) at base of a single intrusive placenta. Seeds few, curved, 3–7 mm long, 1.5–4 mm wide; testa bony and ornamented . . . . . ***Epipremnum***
  - 3b. Ovules solitary, placentation basal. Fruits with a solitary seed . . . . ***Scindapsus***

1b. Spathe in bud slender, long-slender-pedunculate, conspicuously long-beaked (beak to 1/3 length of entire spathe), opening with inside greenish white or white and conspicuously glossy-waxy. Flowers with a membranous perigon of fused tepals. Infructescence with discrete, truncate berries ripening red or orange. Trichosclereids absent . . . . . ***Anadendrum***

Amydrium Schott, *Ann. Mus. Bot. Lugduno-Batavum* 1: 127. 1863; Mayo, Bogner & Boyce, *Genera of Araceae* 116–118, pl.13 & 113A. 1997. **Plate 3**.

Sparse trichosclerieds, net-veined, pinnate and perforated leaf laminae, and white discrete berries readily separate *Amydrium* from all other Monsteroideae.

Taxonomy — World

Five species in tropical and subtropical East Asia from Myanmar to S.W. China as far east as New Guinea

Taxonomy — Borneo

1 species in Borneo, not endemic.

Ecology

Primary and secondary perhumid broad-leaf tropical forests, less often in tropical kerangas, at low to moderate altitudes. On a variety of geologies including limestone.

Anadendrum Schott, *Bonplandia (Hannover)* 5: 45. 1857; Mayo, Bogner & Boyce, *Genera of Araceae* 113, pl.11. 1997. **Plate 4**.

Unlike the remainder of the Monsteroideae *Anadendrum* lacks trichoschlereids. Using floral characters *Anadendrum* is a singular genus in having each flower with a membranous perigone of fused tepals. Confusion between *Pothos* and *Anadendrum* is possible, although the leaf with

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to the pollinating Ruteline scarab beetles. **C.** Detail of post-anthesis female flower zone and lowermost part of the male flower zone; the black lines are fly larvae **D.** Spadix at female anthesis, spathe artificially opened; note the resin droplets of the spadix and also the resin exuded from the cut spathe. **E–F.** Post anthesis spadix showing extensive beetle damage to the sacrificial interpistillar and interstice staminodes.

Plate 13. **Aroideae: Homalomeneae: *Homalomena* Homalomena Supergroup. A–C:** *Homalomena expedita* A.Hay & Hersc. **A.** Plants in habitat at type locality, Batang Kayan. **B.** Detail of emerging shoots on margins of colony. **C.** active leafy shoot with precursor stolon (to left of shoot) and developing new rhizome (to right).

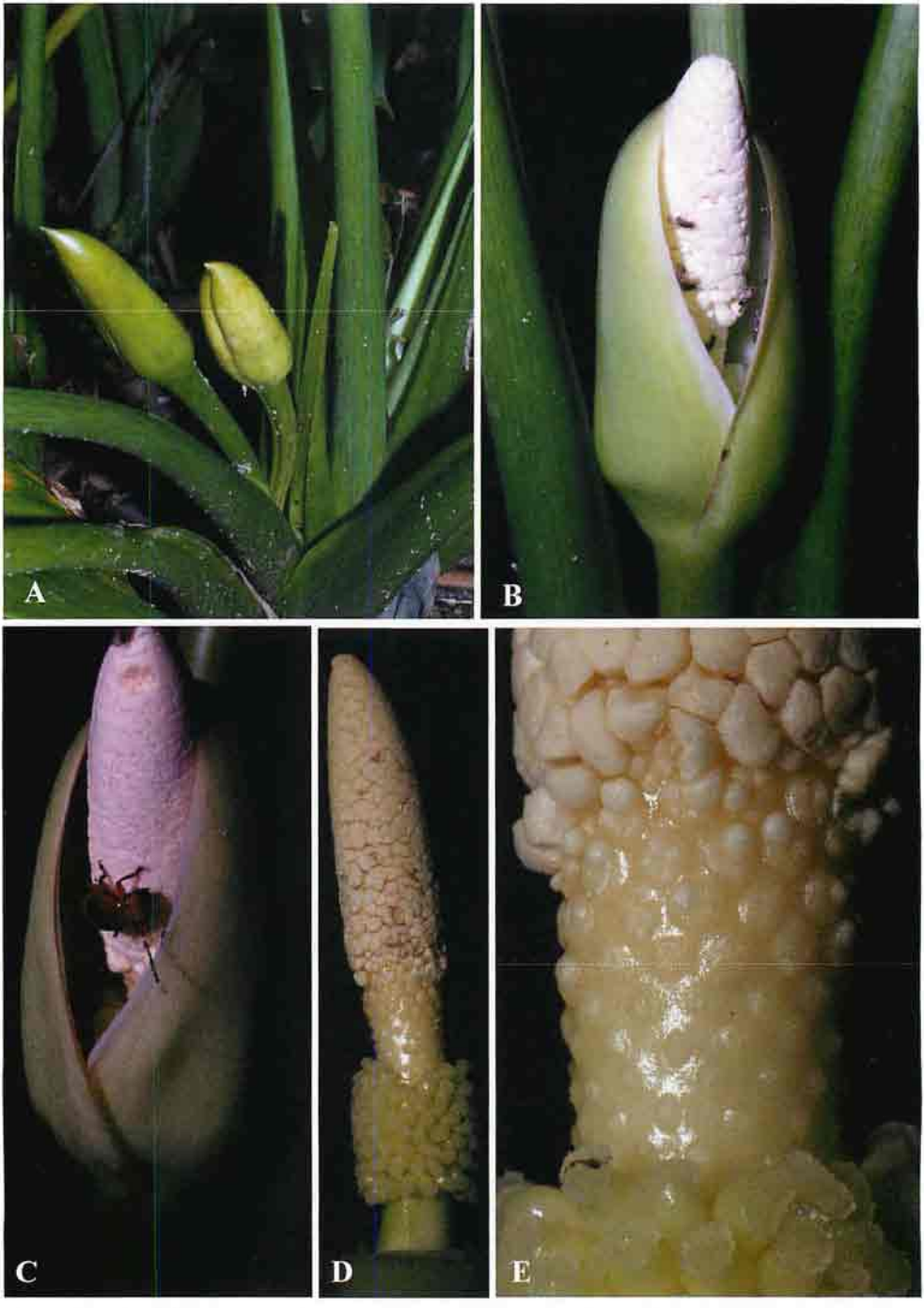

Plate 14. **Aroideae: Homalomeneae: *Homalomena* Homalomena Supergroup. A–E:** *Homalomena expedita* A.Hay & Hersc. **A.** Active shoot with two post anthesis inflorescences (oldest to the right) and prophyll subtending reiterative axis of active shoot. **B.** Inflorescence at female anthesis. Note the numerous *Colocasiomyia* (Diptera,

intramarginal veins crossing the primary venation immediately distinguishes *Pothos*. Furthermore, the inflorescences of *Anadendrum* are produced in distinctive fans at the tips of clinging shoots whereas virtually all *Pothos* produce inflorescences on free lateral branches. Fruiting *Anadendrum* and *Pothos* are superficially similar in producing red or orange berries. However, those of *Anadendrum* are apically truncate with a conspicuous transverse linear stigma, whereas *Pothos* has ellipsoid to globose berries with a tiny, punctiform stigma.

Taxonomy — World

At least 30 species in tropical and subtropical east Asia, from Myanmar to SW China as far east as the Philippines. Many species in Sunda are as yet undescribed.

Taxonomy — Borneo

Perhaps 20 species in Borneo, virtually all undescribed.

Ecology

Primary and secondary perhumid broadleaf tropical forests, at low to moderate altitudes. At least some species are limestone-obligates.

Epipremnum Schott, *Bonplandia (Hannover)* 5: 45. 1857; Mayo, Bogner & Boyce, *Genera of Araceae*, 120–121, pl.15 & 109C. 1997; Boyce, *Blumea* 43: 183–218. 1998. **Plate 5**.

Taxonomy — World

Approximately 15 species occurring throughout tropical Asia from NE India to the Ryukyu Islands southwards to eastern Australia (Queensland) and Oceania (Cook Islands: Rarotonga).

Taxonomy — Borneo

Two species. One (*E. falcifolium* Engl.) endemic.

Ecology

Low to mid-elevation perhumid broadleaf tropical forest, occasionally persisting in disturbed areas or growing lithophytically in exposed situations. The widespread *Epipremnum pinnatum* is associated exclusively with limestone in its few (E. Sabah) localities in Borneo, although elsewhere in its range it is not a limestone obligate.

Rhaphidophora Hassk. *Flora* 25(2 Beibl. 1): 11. 1842; Mayo, Bogner & Boyce, *Genera of Araceae* 118–121, pl. 15 & 109C; Boyce, *Gardens' Bull. Sing.* 53: 19–74. 2001; 57: 211–216. 2005; 58(1): 1–5. 2006; 58(1): 19–24. 2006. **Plate 6**.

Taxonomy — World

About 100 species from wet tropical Africa, and throughout tropical South and South East Asia, perhumid and everwet subtropical and tropical Australia, and the tropical Pacific with extensions into the

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Drosophilidae). **C.** Inflorescence at onset of male anthesis with a solitary (Chrysomelidae: *Dercetina*?). The damage to the male portion of the spadix is typical for chrysomelid visited inflorescences. Note the lack of a spathe constriction. **D.** Spadix at female anthesis with spathe artificially removed. Note the distinctive warty texture of much of the sterile interstice. **E.** Detail of the sterile interstice. The morphology of the warts and their transitional morphology through staminodes to functional male flowers suggest that they are aborted stamens.

subtropical Himalaya, southern China, and the southernmost islands of Japan.

Taxonomy — Borneo

Sixteen species. Six endemic.

Ecology

Usually in well drained subtropical and tropical perhumid to everwet broadleaf subtropical and tropical forest at low to mid-montane elevations, less often in peat swamp or freshwater swamp tropical forest.

Notes

Preliminary revisionary work for Borneo (Boyce, 2001, 2005, 2006a, 2006b) has revealed 16 species in Borneo, of which 6 are endemic. However, much remains to be done, notably with the Hongkongensis Group which undoubtedly comprises a considerable number of undescribed species.

Scindapsus Schott in H.W.Schott & S.L.Endlicher, *Melet. Bot.* 21 1832; Mayo, Bogner & Boyce, *Genera of Araceae* 121, pl. 16 & 109D. 1997. **Plates 7, 8.**

Taxonomy — World

Perhaps as many as 60 species, with about half yet to be described, throughout tropical Asia from NE India though New Guinea to eastern Australia (Queensland).

Taxonomy — Borneo

Perhaps 30 species, at least 10 yet to be described.

Ecology

Usually in well drained subtropical and tropical perhumid to everwet broadleaf subtropical and tropical forest at low to mid elevations.

Notes

There is no modern account for *Scindapsus* and many of the existing species are known from fragmentary collections. The plants are variable in appearance, including colossal high-climbing primary hemiepiphytes (e.g. *S. latifolius* M.Hotta), almost shrubby secondary hemiepiphytes (notably the *S. coriaceus* complex—in which many of the novel Bornean species occur), and the perching litter-trapping epiphytes of the *S. beccarii* complex.

Subfamily Lasioideae

The lasioids are slender to massive, usually solitary or clump-forming stoutly rhizomatous and sometimes stoloniferous herbs with large hastate to sagittate, rarely pinnately-divided leaves on prickly, often mottled petioles to 3 m long. Three genera in Borneo, with two, *Cyrtosperma* Griff. and *Lasia* Lour. commonly found in marshy open grassland close to habitation, while the third, *Podolasia* N.E.Br., is restricted to seasonally inundated broadleaf forest on deep peat deposits.

KEY TO THE GENERA OF BORNEAN LASIOIDEAE

1a. Stems suffruticose, erect to decumbent, usually with prickly conspicuous internodes; leaves hastate to (4×)pinnatifid; spathe caducous, rarely marcescent; placentation apical; fruit usually spinulous . . . . ***Lasia***

1b. Stem a condensed rhizome, rarely with distinct internodes, and these then unarmed; leaves entire, sagittate to hastate; spathe persistent to marcescent; placentation not apical; fruit smooth

2a. Spathe interior white, infructescence nodding, fruits barely emerging from between the tepals, ripening dull purple. Seeds crested or warty. Plant with spines mixed straight and up-turned . . . . . ***Cyrtosperma***

2b. Spathe interior red-purple, infructescence erect, fruits emerging fully from between the tepals, ripening bright red. Seeds smooth. Plant with

spines mixed straight and down-turned . . . . . ***Podolasia***

Cyrtosperma Griff., *Not. Pl. Asiat.* 3: 149. 1851; Hay, *Blumea* 33(2): 428–457.1988; Mayo, Bogner & Boyce, *Genera of Araceae* 138, pl. 26 & 112A. 1997. **Plate 9**.

Cyrtosperma is a genus of large to massive rhizomatous herbs with mottled and usually heavily armed petioles and hastate to sagittate leaves. Inflorescences are solitary and carried on a peduncle similar to the petioles. The majority of *Cyrtosperma* occur in Papuasia, with only one or two species in Borneo. The most commonly met with is *C. merkusii* (Hassk.) Schott, a large plant (2 m or more tall) plant almost always found in open swampy places in association with habitation, has leaves held erect and petioles normally only lightly armed. Occasionally, much more heavily armed smaller plants with spreading leaves are encountered in wet areas in forest, often along water courses, and these equate to *C. ferox* N.E.Br. The most recent revision (Hay, 1988) merges *C. ferox* and *C. merkusii*, although in Sarawak at least they are consistently distinct in terms of morphology and ecology.

Taxonomy — World

About 13 species in tropical southeast Asia as far east as Oceania, with the majority restricted to Papuasia

Taxonomy — Borneo

Two species. Neither endemic.

Ecology

Lowland freshwater swamp forest margins, sometimes persisting in flooded pasture, or in swampy areas of lowland perhumid broadleaf evergreen tropical forest, sometimes on kerangas.

Lasia Lour. *Fl. Cochinch.* 1: 64, 81. 1790; Hay, *Blumea* 33(2): 459–463.1988; Mayo, Bogner & Boyce, *Genera of Araceae* 138, pl. 26 & 112A. 1997; Hambali & Sizemore, *Aroideana* 20: 37–39. 1997. **Plate 10**.

Lasia is a genus of clumping or colonial often stoloniferous herbs with a thick prickly creeping or unarmed erect stem. The prickly petioles carry either sagittate to hastate-sagittate (the latter mainly in juveniles) to deeply simply to 4× pinnatifid leaves. The spathe is notably thick and somewhat spongy and either twisted and opening basally (*L. spinosa* (L.) Twaites) or straight and opening terminally (*L. concinna* Alderw.). *Lasia spinosa* is widespread and often common in Borneo, as well as being variable in habit, from erect and clump-forming to somewhat decumbent and colonial via the production of long stolons, with leaves varying from simple hastate to pinnatifid. By comparison *L. concinna* appears to be restricted to the Kupuas river valley in Kalimantan (Indonesian Borneo) and with the widely separated populations remarkably morphologically stable.

Taxonomy — World

Two species; one (*L. spinosa*) widespread in tropical Asia from India to New Guinea, the other (*L. concinna*) endemic on Borneo.

Taxonomy — Borneo

Two species. One (*L. concinna*) endemic.

Ecology

Lowland freshwater swamp forest margins, sometimes persisting in seasonally flooded pasture and *padi* where it is often maintained as a vegetable—*paku longkan* —with the newly emerging shoots being picked and fried with *belacan* (shrimp paste).

Podolasia N.E.Br., *Gard. Chron.*, n.s., 1882(2): 70. 1882; Hay, *Blumea* 33(2): 463–465.1988; Mayo, Bogner & Boyce, *Genera of Araceae* 138, pl. 26 & 112A. 1997. **Plate 11**.

Plate 15. **Aroideae: Homalomeneae: *Homalomena* Chamaecladon Supergroup. A–C:** *Homalomena humilis* (Jack) Hook.*f*. **A.** Flowering plant, red foliage expression; **B.** Plant with inflorescences at various stages of development, the sequence running from right (youngest) to left (oldest). Note the small size of the spathes and the lack of a constriction. **C.** Detail of inflorescence at female anthesis; note that spadix is fertile to the tip and that the flowers have two anthers.

The richly colored spathe and spadix becoming bicolored as male anthesis progresses are diagnostic. The spadix begins white, and remains white through female anthesis. At the onset of male anthesis (which proceeds from the tip to the base of the spadix) the individual flowers turn to deep purple as male anthesis proceeds. By the end of anthesis and throughout fruit development, the spadix is deep purple.

Podolasia may be distinguished vegetatively by the short, distinct, unarmed internodes, the persistent leaf bases (often decaying into tough fibers), through which adventitious roots emerge, and by the downward-pointing petiole prickles. The fruits are also characteristic, being relatively very large (their length considerably exceeding the diameter of the spadix), individually distinct berries exserted well clear of the tepals. *Podolasia stipitata* is very sporadic in distribution throughout its range, although it is frequently locally abundant.

Taxonomy — World

One species occurring disjunctly in Sumatera, Peninsular Malaysia, and Borneo

Taxonomy — Borneo

See above.

Ecology

Lowland peatswamp forest, usually on slightly raised peat deposits (podzols) but still subject to seasonal inundation.

Subfamily Aroideae

The Aroideae comprises all genera with naked unisexual flowers, and thus all taxa are monoecious (very rarely paradioecious —*Arisaema*). The Aroideae in Borneo comprises 11 tribes.

Tribe Homalomeneae

Two very closely allied genera in Asia, *Homalomena* Schott and *Furtadoa* M.Hotta, mostly with strongly aromatic (terpenoids) tissues and spathes fully persistent to fruit maturity. *Homalomena* is widespread throughout tropical and subtropical Asia, with significant centers of endemism on Sumatera, Borneo, and New Guinea. *Furtadoa* is restricted to Sumatera and Peninsular Malaysia and differs from *Homalomena* primarily by each staminate flower with an associated pistillode.

Species of *Homalomena* are frequently confused with *Schismatoglottis*, although the infructescences of *Homalomena*, in which the spathes wholly persistent to fruit maturity, and then split basally and upwards to reveal the fruits, are very different from those of *Schismatoglottis* in which the spathe limb is shed, often while still fresh, during anthesis, while the lower spathe persists into fruiting as a barrel-shaped to ellipsoid covering, splitting from the top downwards to release the ripe fruits.

Homalomena Schott in H.W.Schott & S.L.Endlicher, *Melet. Bot.*: 20. 1832; Boyce, *Kew Bull.* 49(4): 793–80. 1994; Mayo, Bogner & Boyce, *Genera of Araceae* 177–180, pl. 47i-ii & 117A. 1997; Hay & Herscovitch, *Gardens' Bull. Sing* 54: 171–178. 2002; Boyce & Wong, *Gardens' Bull. Sing.* 60(1): 1–29. 2008; Boyce & Wong, *Webbia* 64(2): 169–173. 2009; Boyce, Wong & Fasihuddin, *Gardens' Bull. Sing.* 61(2): 29–78. 2010. **Plates 12–15**.

Homalomena is the most speciose aroid genus in Borneo, with in excess of 350 species, of which fewer than 20 have been described. The genus comprises minute to very large clumping, tufted, rarely creeping, and very rarely climbing mostly strongly aromatic herbs with cordate to lanceolate leaves. Inflorescences generally open for only a few hours before closing again and then soon becoming pendulous with the spathe persisting, and occasionally becoming brightly colored, around the developing infructescence.

Bornean *Homalomena* divide into three morphotaxa (morphologically cohesive but phylogenetically untested higher taxa) termed 'supergroups' (see Boyce & Wong, 2008): Homalomena, Chamaecladon &

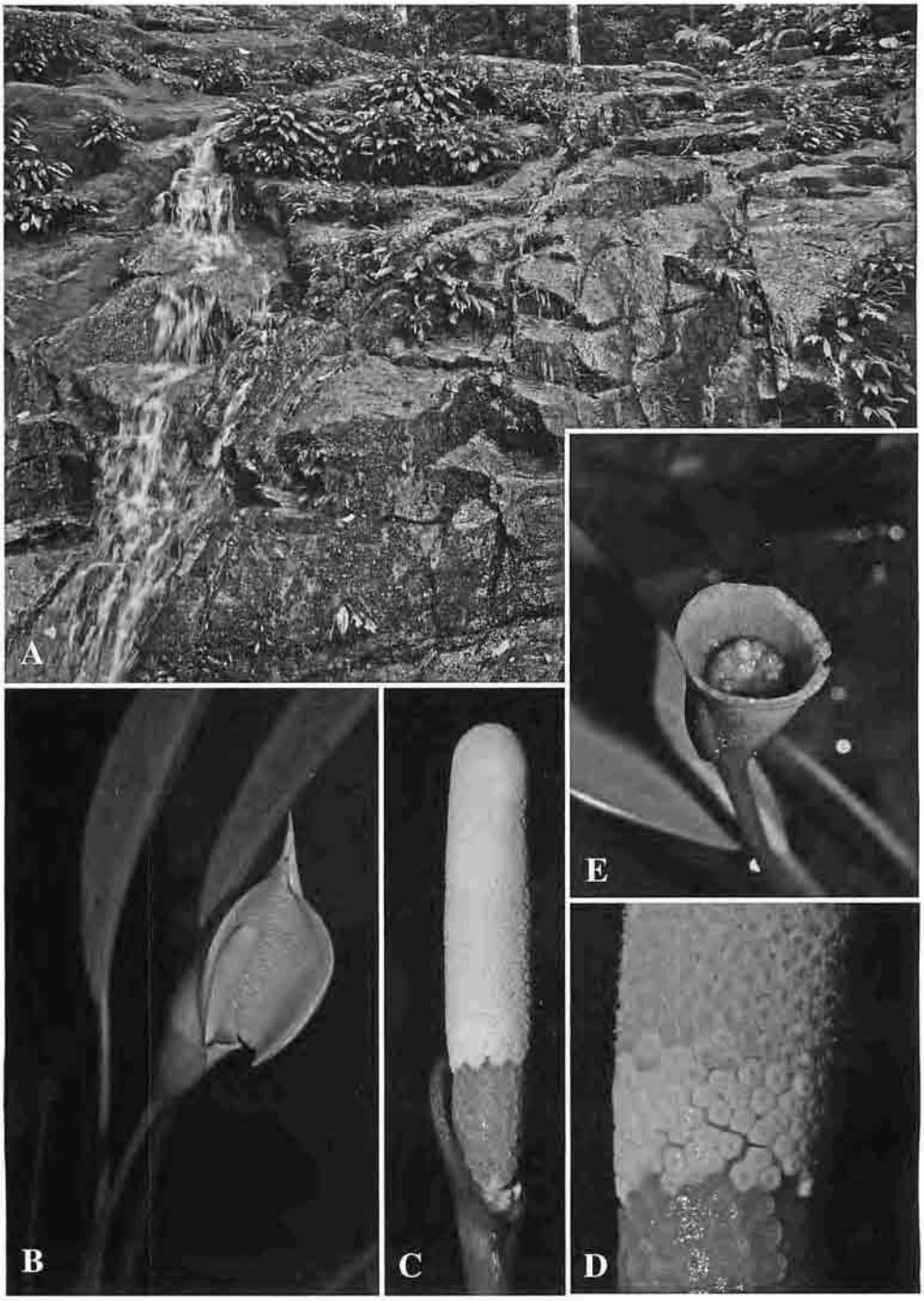

Plate 16. **Aroideae: Schismatoglottideae: *Aridarum* Ridl. A–E:** *Aridarum nicolsonii* Bogner. **A.** Plants in habitat on a sandstone waterfall at Santubong, NW Sarawak. The photograph was taken during dry weather. In wet weather this waterfall becomes a raging torrent with the *Aridarum* directly in the water flow. **B.** Flowering plant. Note that the

Cyrtocladon. The Bornean supergroups are defined by the following characters:

The Homalomena supergroup comprises medium to large creeping to erect plants with strongly aromatic tissues, pleionanthic, or rarely hapaxanthic, shoot modules and spathes greater than 1.5 cm long, with no or only a very weak constriction between the upper and lower spathe. Spathe movement during anthesis, where known, comprises simple gaping and then closing of the spathe limb, no spadix movements have been recorded. Ovary three to four locular. Staminate flowers with three to four, rarely five to six, anthers.

The Chamaecladon supergroup comprises small to minute often creeping, less often erect plants with odorless, or very rarely aromatic, tissues; as far as is known only pleionanthic shoot modules, and spathes less than 1 cm, very rarely up to 1.5 cm long, with no constriction between the upper and lower spathe. Spathe movement during anthesis, where known, comprises simple gaping and closing of the spathe limb. No spadix movement recorded. Ovary two to three locular. Staminate flowers with two to three anthers.

The Cyrtocladon supergroup comprises medium to very large erect to creeping plants with strongly aromatic tissues, pleionanthic (but very few studied) shoot modules and spathes greater than 2 cm long, with weak to moderate to pronounced constriction between the upper and lower spathe. All of the several species so far studied undergo a complex series of spathe and spadix movements during anthesis. Ovary three to four locular. Staminate flowers with three to four, rarely five to six, anthers.

Taxonomy — World

Indo-Malesia to southern China eastwards to the Solomon Islands with centers of diversity in Sumatera, Borneo and New Guinea; ca. 8 Neotropical species (section *Curmeria* but generic status very doubtful).

Taxonomy — Borneo

At least 350 species, most undescribed.

Ecology

Primarily understory herbs in lowland evermoist to everwet, or less often perhumid, tropical or subtropical broadleaf forest, but also reaching mid-montane zone; sometimes rheophytic, very rarely helophytic, occasionally relictual in regrowth and along road cuttings.

Tribe Schismatoglottideae

The Schismatoglottideae is a diverse group of terrestrial, rheophytic, lithophytic or chasmophytic rainforest herbs centered on Borneo. *Schismatoglottis* Zoll. & Moritzi is by far the largest genus, extending throughout Malesia to the tropical western Pacific, north through much of Indochina and into SW China and Taiwan. The remaining genera are relatively small to monospecific and with the exception of *Hestia* S.Y.Wong & P.C.Boyce, *Apoballis* Schott, and *Piptospatha* N.E.Br. are endemic on Borneo.

Schismatoglottis is predominantly non-rheophytic, although it does comprise some rheophytic species, most of which are notable for the petiolar sheath being

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spathe limb is beginning to shed while still fresh. **C.** Spadix revealed by artificially removing the spathe. **D.** Detail of the spadix showing the pistillate flowers (below, green), the zone of pistillodes (ivory) and a portion of the staminate flower zone (cream). Note the excavated anthers and the thecae horns. **E.** Persistent lower spathe forming a splash-cup around the developing fruits.

Plate 17. **Aroideae: Schismatoglottideae: *Bakoa* P.C.Boyce & S.Y.Wong. A–D:** *Bakoa lucens* (Bogner) P.C.Boyce & S.Y.Wong. **A**, Plants in habitat, Bako N.P., NW Sarawak. **B.** Plant with inflorescence at the onset of female anthesis. Note that spathe opening is facing downwards. **C.** Inflorescence at female anthesis. Note that the spathe barely opens. **D.** Inflorescence (spathe artificially removed). Note that the greater portion of the spadix is adnate to the spathe.

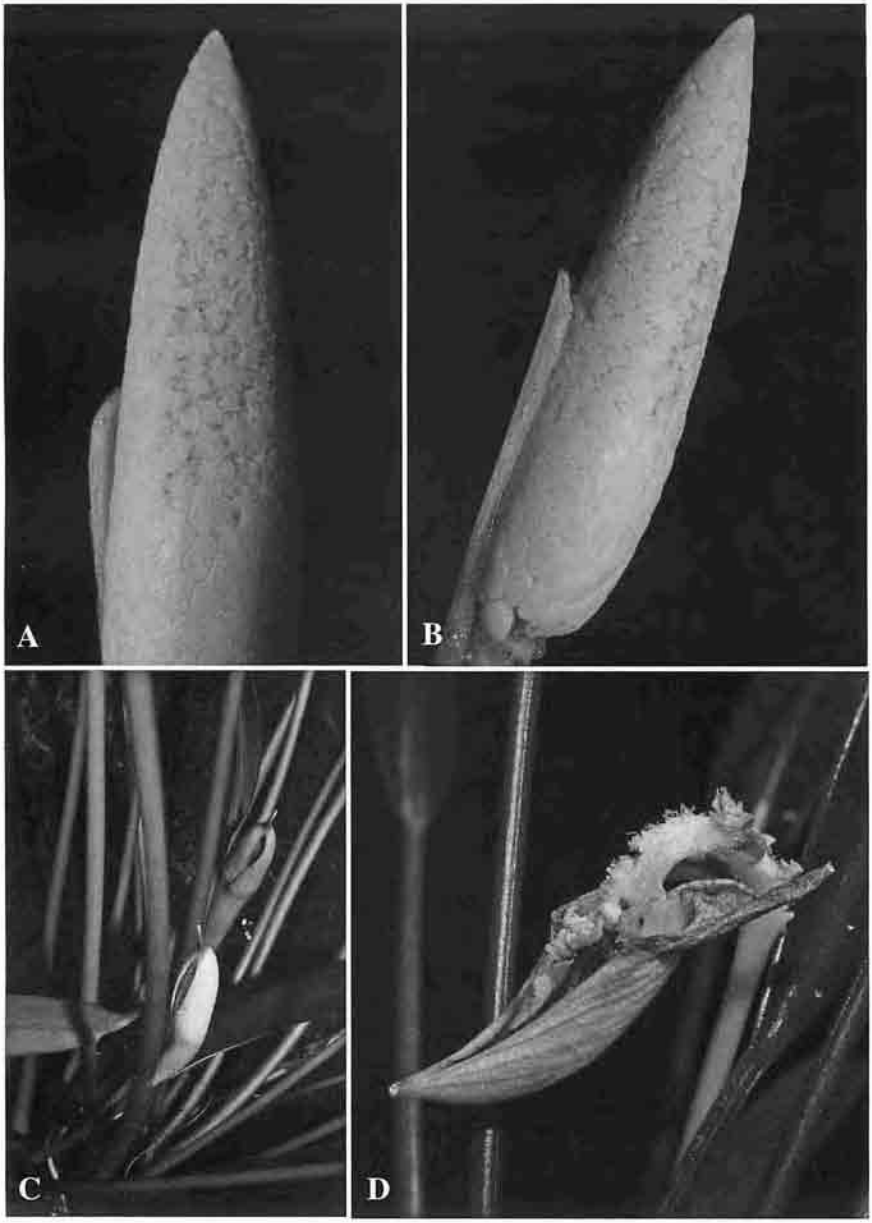

Plate 18. **Aroideae: Schismatoglottideae: *Bakoa* P.C.Boyce & S.Y.Wong. A–E:** *Bakoa lucens* (Bogner) P.C.Boyce & S.Y.Wong. **A & B.** Spadix just prior to male anthesis. Note that the fertile staminate flowers occupy only a small portion of the spadix, roughly adjacent to the opening of the spathe limb. **C.** Plant with inflorescence at late anthesis white with green (acuminate tip; spadix brown) and at fruit mid-maturation (spathe green and thickened). **D.** Infructescence c. half way through fruit dispersal. Note that reflexed spathe torn away from the peduncle but distally still convolute and clasping the spent spadix.

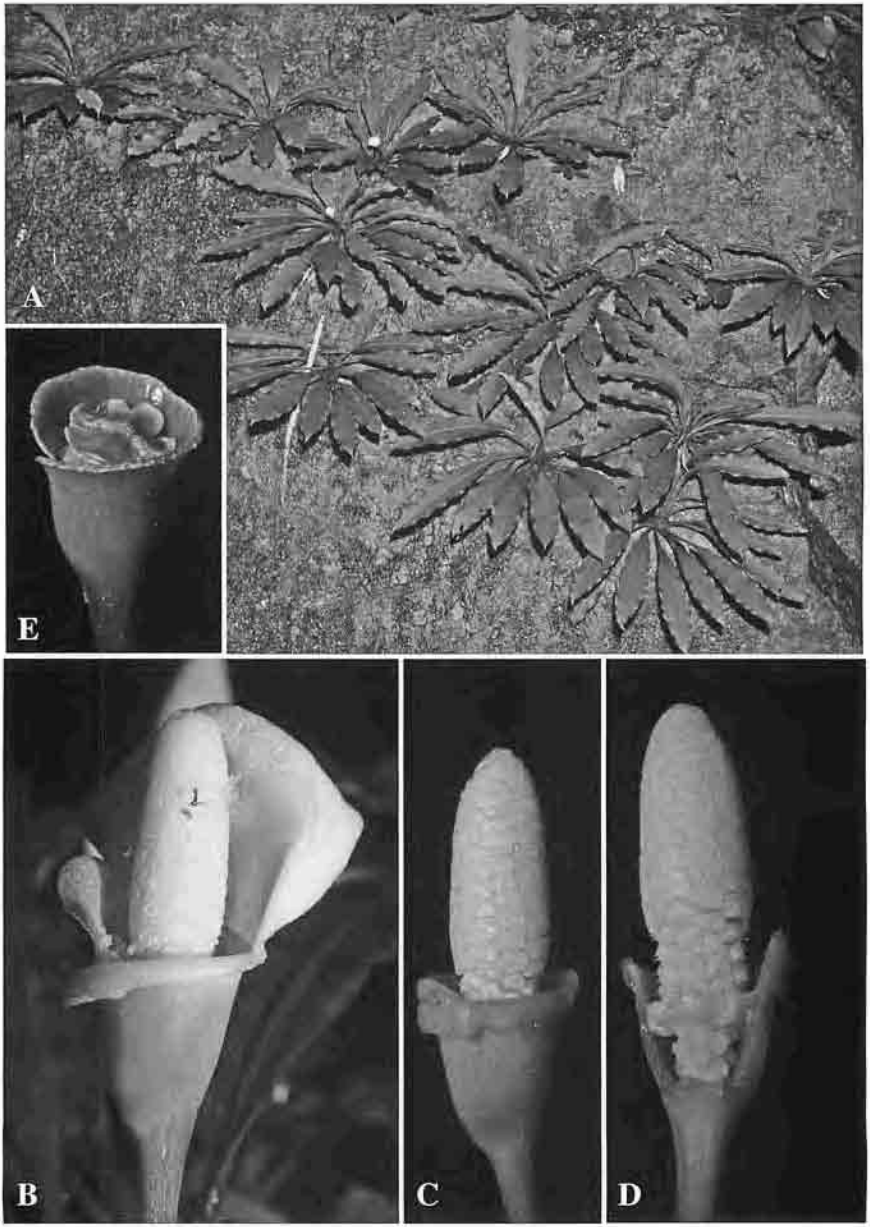

Plate 19. **Aroideae: Schismatoglottideae: *Bucephalandra* Schott. A–E:** *Bucephalandra motleyana* Schott. **A.** Plants in habitat on argillaceous limestone river boulders. **B.** Inflorescence at early onset of male anthesis, spathe limb beginning to shed. **C.** Inflorescence during male anthesis, spathe limb shed. **D.** Inflorescence during male anthesis with portion of lower spathe removed. Note the conspicuous thecae horns to the staminate flowers and that the shield-like staminodes have lowered to seal off the pistillate flower zone. **E.** Infructescence showing the persistent lower spathe forming a splash cup. Note the shield-like staminodes have hardened and become photosynthetic and are functioning to protect the developing fruits.

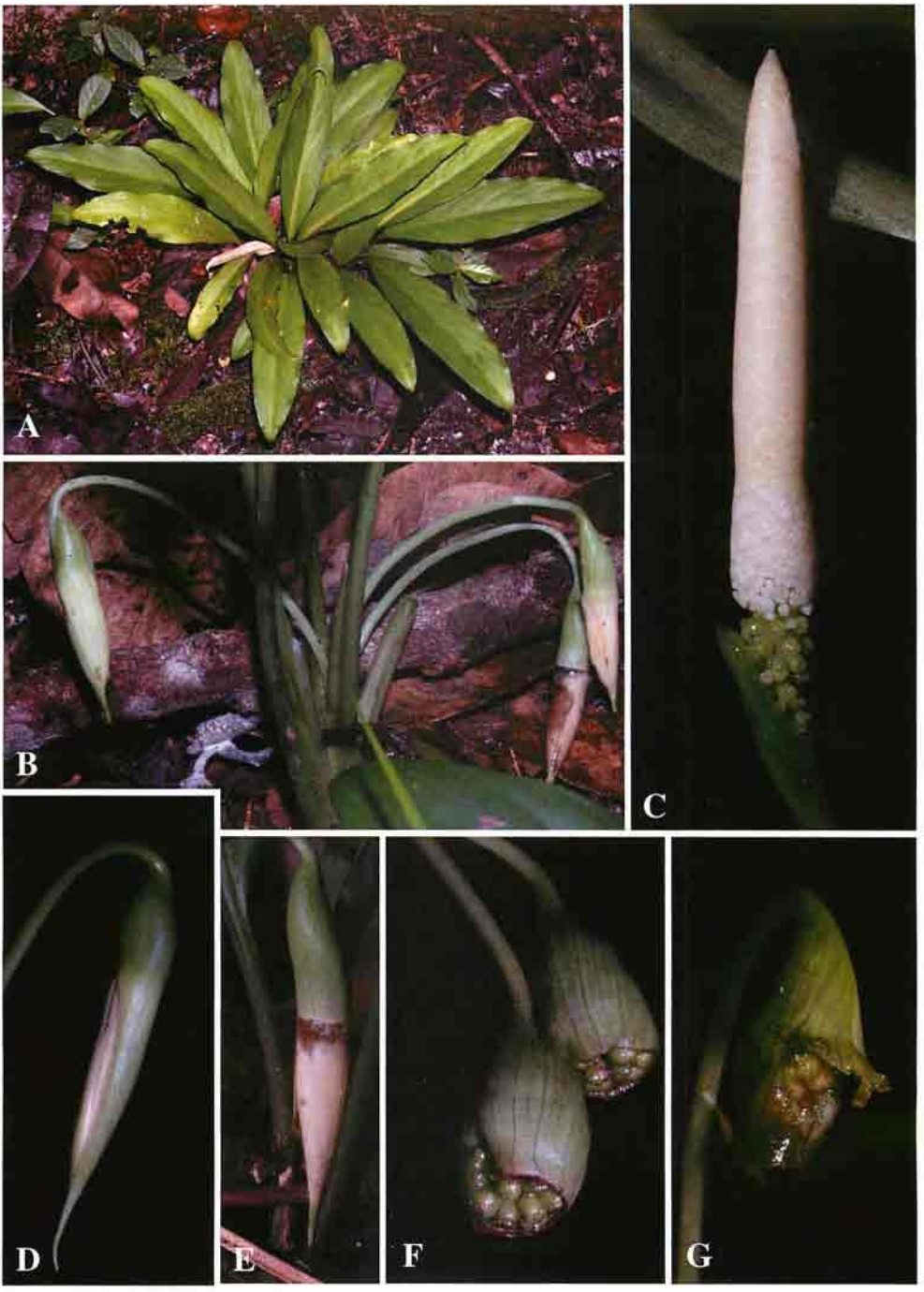

Plate 20. **Aroideae: Schismatoglottideae: *Hestia* S.Y.Wong & P.C.Boyce. A–G:** *Hestia longifolia* (Ridl.) S.Y. Wong & P.C. Boyce. **A.** Plant in habitat on podsol. **B.** Nodding inflorescences, the inflorescence to the left at female anthesis; upper right at male anthesis, lower right post-anthesis with spathe beginning to degrade prior to being shed. **C.** Spathe

attached only at the very base, with the remainder forming a long, variously persisting, free-ligular portion. This peculiar morphology, while present in a minority of *Schismatoglottis*, is common to all except two of the remainder of the tribal genera, and which are in turn all obligate or facultative rheophytes.

KEY TO THE GENERA AND MAIN GENERIC DIVISIONS OF BORNEAN SCHISMATOGLOTTIDEAE

1a. Wings of petiolar sheath fully or almost fully attached to the petiole, if free ligular then foliage leaves arranged distichously; seeds never with a micropylar appendage
  2a. Inflorescences on very slender peduncles, nodding at anthesis, peduncle at spathe insertion flexing 180° from vertical axis. Infructescences narrowly campanulate, nodding. Plants of podsols . . . . . ***Hestia***
  2b. Inflorescences erect to nodding at anthesis, if nodding, then either peduncle massive, and peduncle at spathe insertion at most 45° from vertical axis. Infructescences fusiform with a constricted orifice, if campanulate, then thick-walled and erect, never nodding. Plants of various substrates but never on podsols
    3a. Modules monophyllous, congested in a distichous arrangement; ligular free sheath persistent . . . . . ***Pichinia***
    3b. Modules polyphyllous, never distichous; petiolar sheath fully attached, persistent or marcescent . . . . . ***Schismatoglottis***
1b. Wings of petiolar sheath always extended into a free ligular portion; seeds sometimes with micropylar appendage
  5a. Spathe not constricted; plants glabrous
    6a. Thecae of anther never with horn- or needle-like projections
      7a. Spadix almost completely adnate to spathe; staminate flowers mostly sterile with a narrow zone of fertile flowers exposed by the spathe opening; peduncle declinate during fruit maturation but twisting to become semi-erect at fruit maturity; spathe persistent into fruiting, and then at fruit maturity swiftly drying, reflexing and opening basally by tearing at peduncle insertion to expose fruits but remaining distally convolute and while in this situation clasping the spadix. Seeds with blunt micropyle . . . . . ***Bakoa***
      7b. Spadix either entirely free or only part of the pistillate flower zone which is adnate to spathe; staminate flowers all fertile; peduncle erect (and then spathe limb caducous) or declinate (and spathe persistent) throughout the fruit dispersal; spathe limb either caducous early in anthesis or persistent until fruit maturity and then falling, still fresh to reveal entire spadix and ripe fruits. Seeds with a pronounced, hooked, micropylar appendage . . . . . ***Piptospatha***
    6b. Thecae of anther each with a horn- or needle-like projection, although these sometimes visible only after female anthesis

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slightly gaping at female anthesis. **D.** Spadix with the spathe removed artificially to reveal the female and male flower zones. **E.** Inflorescence post-anthesis with spathe limb rotting at junction of lower spathe, later to be shed together with spent part of spadix. **F.** Infructescences with the distinctive narrowly campanulate lower spathe. **G.** Fruits.

8a. Thecae with needle-like projection extending only after female anthesis; projection tipped with a weakly peltate ovate-triangular flap. Appendix composed of pistillodes . . . . . ***Schottariella***

8b. Thecae with a horn- or needle-like projection present prior to female anthesis; with the projection pointed and never associated with a terminal flap. Appendix, where present, composed of staminodes

9a. Sterile interstice of spadix with flattened scale-like staminodes; anthers not excavated. . . . . ***Bucephalandra***

9b. Sterile interstice absent or with truncate staminodes; anthers nearly always with the top excavated (except *A. incavatum*) . . . . . ***Aridarum***

5b. Spathe constricted or if not constricted then plant variously to coarsely hairy

10a. Thecae of anther without horn- or needle-like projections; ovules on parietal placenta; seeds without a micropylar appendage . . . . . ***Schismatoglottis* Multiflora Group**

10b. Thecae of anther, each with horn- or needle-like projections; ovules on basal placenta; seeds with a long, hooked micropylar appendage . . . . . ***Phymatarum***

11a. Stem hapaxanthic. . . . . ***Schismatoglottis* Calyptrata Group**

11b. Stem pleionanthic

12a. Spathe limb mostly caducous

13a. Leaf sheath fully attached to petiole. . . . . ***Schismatoglottis* Calyptrata Group**

13b. Leaf sheath free ligular . . . . . ***Schismatoglottis* Multiflora Group**

12b. Spathe limb marcescent to crumbling and/or deliquescent

14a. Petiole sheathing only at extreme base; each foliage leaf alternating with a cataphyll . . . . . ***Schismatoglottis* Tecturata Group**

14b. Petiole usually sheathing for at least a third of its length (rarely less); foliage leaves not alternating with cataphylls

15a. Inflorescence erect; spathe limb irregularly crumbling and breaking away at or after male anthesis; small to medium plants . . . . . ***Schismatoglottis* Asperata Group**

15b. Inflorescence nodding; spathe limb clasping the spadix and more-or-less marcescent after anthesis, finally falling with spent parts of spadix; massive pachycauls. . . . . ***Schismatoglottis* Corneri Group**

Aridarum Ridl., *J. Bot.* 51: 201.1913; Mayo, Bogner & Boyce, *Genera of Araceae* 192, Pl. 54. 1997; Bogner & Hay, *Telopea* 9(1): 183–194. 2000; Okada, *Acta Phytotax. Geobot.* 57(1): 61–64. 2006. Wong & Boyce, *Gardens' Bull. Sing.* 58(2): 279–286. 2007. **Plate 16**.

Aridarum differs from all other genera in the Schismatoglottideae by the combination of excavated anthers with horns and no morphologically differentiated sterile zone between the staminate and pistillate flower zone.

Taxonomy — World

Nine species all endemic on Borneo.

Taxonomy — Borneo

See above.

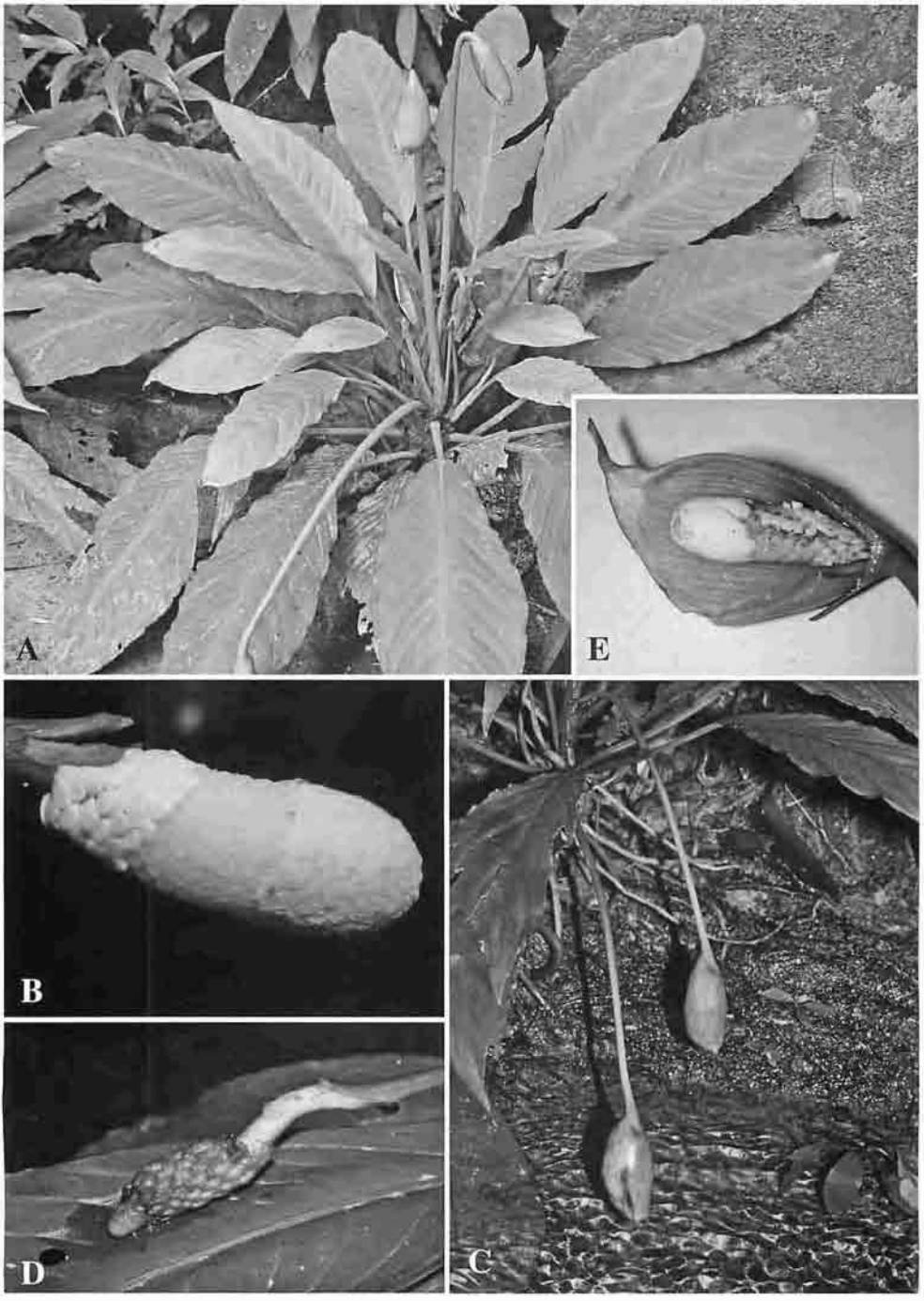

Plate 21. **Aroideae: Schismatoglottideae: *Ooia* S.Y.Wong & P.C.Boyce. A–D:** *Ooia grabowskii* (Engl.) S.Y. Wong & P.C. Boyce. **A.** Plant in habitat on riverine boulder. Note the erect peduncle with the pink spathe nodding at the tip. **B.** Inflorescence with spathe artificially removed to reveal spadix. Note the large zone of ivory white pistillodes at the

Ecology

Primarily obligate rheophytes, sometimes facultative lithophytes or terrestrial in forest, usually in deep shade, from the lowlands to lower montane everwet or perhumid broadleaf forests.

Bakoa P.C.Boyce & S.Y.Wong, *Bot. Stud. (Taipei)* 49(4): 398. 2008. **Plates 17, 18.**

Bakoa was first described in the genus *Hottarum* by Bogner (1983a) and subsequently transferred to *Piptospatha* (Bogner & Hay, 2000), although it sat comfortably in neither genus. Molecular studies by Wong (Wong *et al.*, 2010) highlighted that the several morphological peculiarities found in the species were amply backed up by a unique molecular profile that well-supported the recognition of a separate, new genus, with no close allies.

Taxonomy — World

Two species, one undescribed, both endemic to Borneo.

Taxonomy — Borneo

See above.

Ecology

Obligate rheophytes on exposed rocks on waterfalls in lowland perhumid broadleaf forest.

Notes

The combination of a spadix more than half adnate to the spathe, fertile staminate flowers mostly restricted to a small zone coincidental with the area exposed by the gaping spathe during anthesis, a fully persistent spathe becoming wholly marcescent at fruiting and seeds with a blunt micropyle borne on an annuliform basal placenta is unique in the Schismatoglottideae.

Post pollination the persistent spathe turns green and thickens slightly while the peduncle becomes declinate, holding the spathe with the free margins downwards; as also occurs in *Ooia* S.Y.Wong & P.C.Boyce. At the onset of fruit maturity the peduncle of *Bakoa* twists through 180° and once more becomes semi-erect, bringing the spathe free margins to a dorsal position after which the spathe dries and turns brown very swiftly and thence by reflexing of the 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. The fruiting mechanics of *Bakoa* are unique in the tribe.

Bucephalandra Schott, *Gen. Aroid.*: t. 56. 1858; Bogner, *Aroideana* 3(4): 134–143, figs. 1–15. 1980 & *Pl. Syst. Evol.* 145: 159–164. 1984; Mayo, Bogner & Boyce, *Genera of Araceae* 189, Pl. 52. 1997; Bogner & Hay, *Telopea* 9(1): 195–198. 2000. **Plate 19.**

Bucephalandra is a genus of very small to medium-sized obligate rheophytes endemic on Borneo. One species (*B. motleyana* Schott) is widespread and vegetatively highly variable, while the other (*B. gigantea* Bogner) is known from a single gathering.

Bucephalandra is distinguished from all other genera by the presence of motile shield-shaped white staminodes separating the staminate and pistillate flower zones.

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spadix base, and the pubescent staminate flowers. **C.** Fruiting plant in habitat. Note that the peduncle is declinate from the base to bring the infructescences close to the water, and the persistent spathe has turned green. **D.** Spadix post fruit dispersal. Note the persistent spadix axis with the scars of the fallen flowers. The swollen portion marks the position of the now-shed fruits. **E:** *Ooia kinabaluensis* (Bogner) S.Y.Wong & P.C.Boyce. Note the differences in the arrangement and structure of the flowers compared with *O. grabowskii*. Image **E** © Kohei (Taekenaka) Takano.

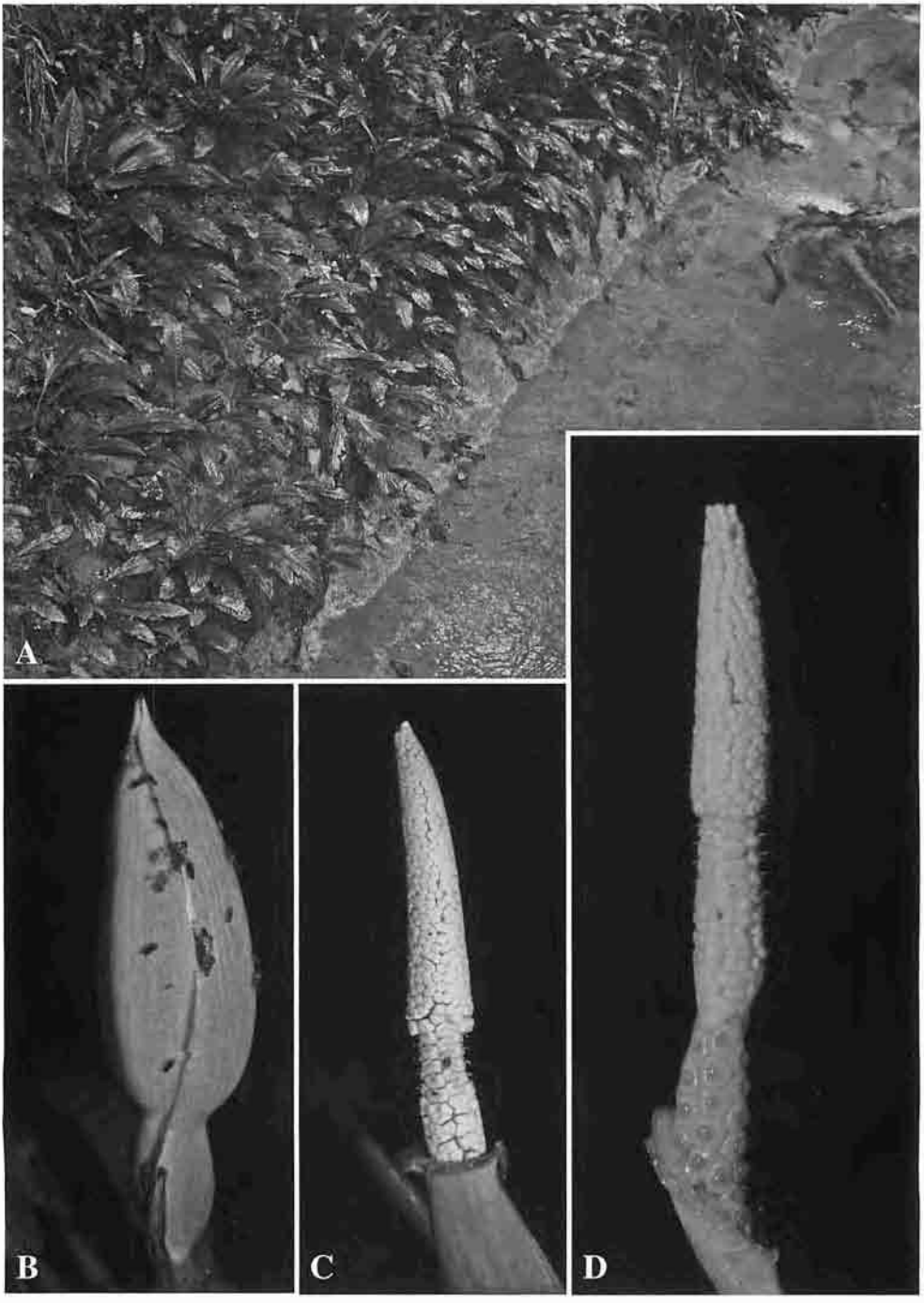

Plate 22. **Aroideae: Schismatoglottideae: *Phymatarum* H.Hotta. A–D:** *Phymatarum borneense* M.Hotta. **A.** Plants in habitat on a muddy river bank subjected to periodic inundation, Mulu N.P., NE Sarawak. **B.** Inflorescence at female anthesis. Note the spathe is only slightly open. At this stage it produces a powerful smell of methyl acetate, which

These staminodes persist, becoming photosynthetic, after flowering and function to seal the persistent cup-shaped spathe to protect the developing fruit.

Taxonomy — World

Two species, both endemic on Borneo.

Taxonomy — Borneo

See above.

Ecology

Obligate rheophytes on exposed rocks in lowland to middle elevation perhumid and everwet broadleaf tropical forest. *Bucephalandra motleyana* is often, but not exclusively, limestone-associated.

Notes

Bucephalandra motleyana was the first rheophytic Schismatoglottideae to be described (Schott, 1858). Beccari (1879) independently described the same species in a new genus, *Microcasia*, believing his plant to be different as he was misled by serious inaccuracies in the Schott's original description. Beccari believed *B. motleyana* to be the smallest of all aroids, true at the time, although that distinction now belongs to species of the genus *Wolffia*, and there are several other Schismatoglottideae that are smaller, including the recently described *Aridarum minimum* H.Okada. Nevetheless, *Bucephalandra* are certainly small, often flowering when only 1 cm tall, and producing an inflorescence decidedly out of proportion to the stature of the plant.

Hestia S.Y.Wong & P.C.Boyce, Bot. Studies (Taipei) in press. **Plate 20**.

A very distinctive genus easily recognized by the rather numerous nodding inflorescences on relatively very long slender wiry peduncles. There is only a weak constriction present between the lower spathe and upper spathe, and the orifice of the lower spathe is open during fruiting. The entire non-pistillate portion of the spadix often dries and adheres to the spathe limb with the whole combined unit shedding.

The sole species, *Hestia longifolia* has vegetative modules that readily disarticulate from the deep-seated rhizome. The function of the disarticulation in this podsol-obligated species is not clear, but it is speculated that it may be an adaption to fire resistance in a highly fire-prone habitat. Perhaps enabling the shoot unit to be destroyed in some way prevents damage to the main perennating system.

Taxonomy — World

One species disjunct between the Malay Peninsula, where it is known to only from Perak, and Borneo, where it occurs in numerous but widely scattered localities in Sarawak and Brunei.

Taxonomy — Borneo

See above.

Ecology

On raised podsols in swampy areas in kerangas formations within lowland and hill perhumid broadleaf tropical forest.

Notes

Hestia longifolia (Ridl.) S.Y.Wong & P.C.Boyce was long placed in *Schismatoglottis*, although highly distinct by vegeta-

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serves to attract the pollinating flies visible on the spathe exterior. The damage to the spathe is due to chrysomelid beetles. **C.** Inflorescence at male anthesis. The spathe limb already shed. **D.** Inflorescence at female anthesis with spathe artificially removed. Note the conspicuous stigmatic droplets, the verrucate fertile and sterile staminate flowers and thecae horns on the fertile flowers.

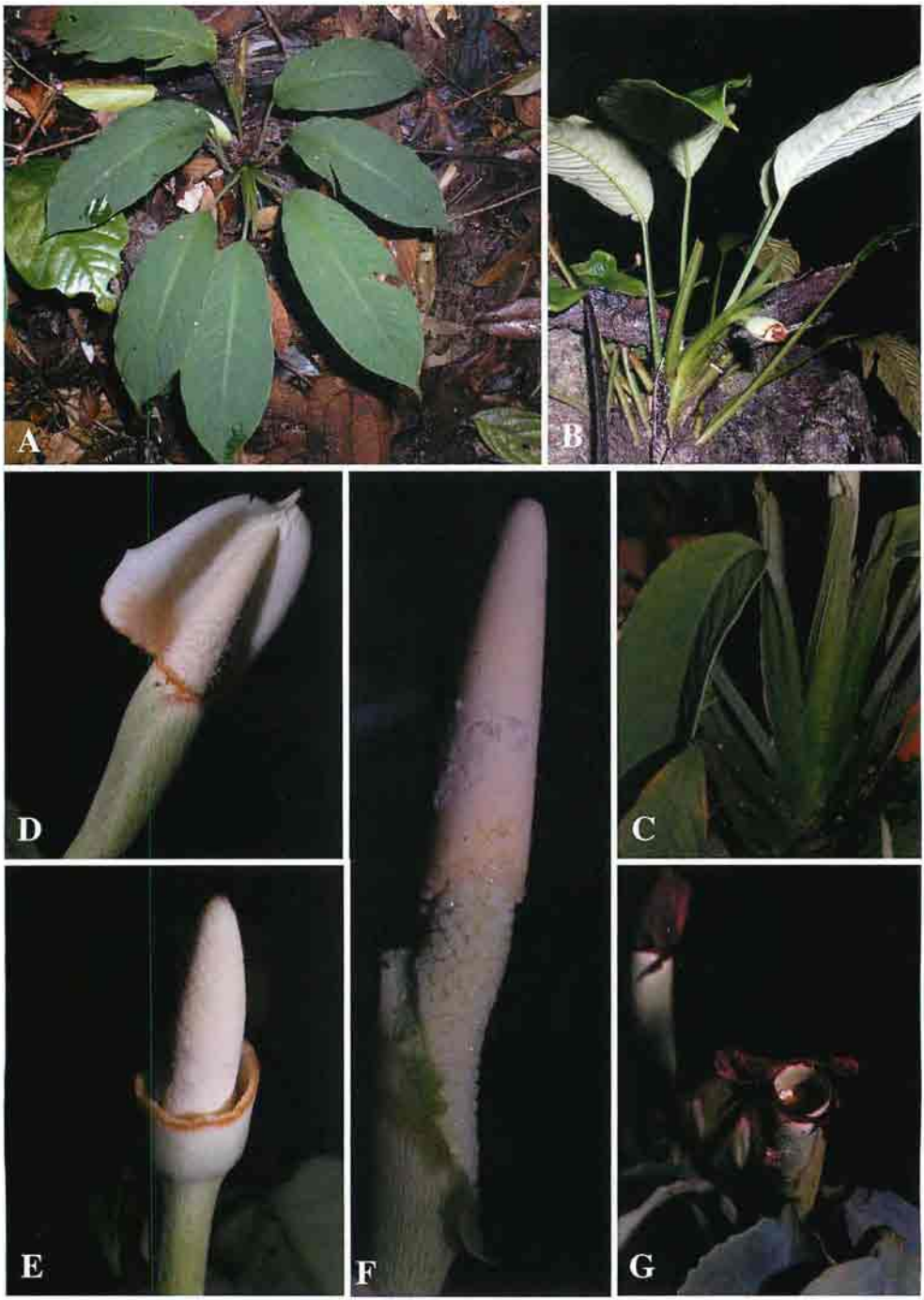

Plate 23. **Aroideae: Schismatoglottideae: *Pichinia* S.Y.Wong & P.C.Boyce. A–G:** *Pichinia disticha* S.Y. Wong & P.C. Boyce. **A.** Plant in habitat, note the distichous leaf arrangement. **B.** Plant in habitat showing the leaf lamina glaucous abaxially and persistent free-ligular petiolar sheaths. **C.** Cultivated plant showing detail of the leaf arrangement.

tive morphology and in the form of the inflorescences. Molecular work by Wong (Wong *et al.*, 2010) demonstrated without doubt that *S. longifolia* was misplaced in *Schismatoglottis*, and also distinct from all other genera in the Schismatoglottideae.

Ooia S.Y.Wong & P.C.Boyce, *Bot. Stud. (Taipei)* in press. **Plate 21**.

Ooia is a recently erected genus removed from formerly heterogeneous *Piptospatha* N.E.Br (where it was treated as in formal taxon—Grabowskii Group—by Bogner & Hay (2000). While the nodding pink inflorescences superficially resemble those of *Piptospatha*, numerous features of the flowering and fruiting mechanics are highly individual, including the almost wholly persistent spathe, the persistent spadix axis, and the shedding of the pistillate and sterile flowers post-anthesis. Molecular evidence also strongly supports the removal of *Ooia* from *Piptospatha*.

Taxonomy — World

Two or perhaps three species, all endemic on Borneo.

Taxonomy — Borneo

See above.

Ecology

Obligate or facultative rheophytes, occasionally lithophytic, along streams and by waterfalls in lowland to lower montane perhumid to everwet broadleaf tropical forest.

Notes

Ooia is unique in the tribe as so far observed by the persistence of the entire spadix axis through to fruit maturation and dispersal, with the entire axis remaining fresh and the non-pistillate flowers sloughing away; indeed this is unique in the family. The spathe of *Ooia* is persistent late into fruit development at which point the extreme top margin and associated rostrum 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. Such inflorescences are pendent and often with their tips submerged in water.

Phymatarum M.Hotta, *Mem. Coll. Sci. Kyoto Imp. Univ., Ser. B, Biol.* 32(1): 29. 1965; Bogner, *Pl. Syst. Evol.* 144: 59–66. 1984; Mayo, Bogner & Boyce, *Genera of Araceae* 189, Pl. 53, 118C. 1997; Bogner & Hay, *Telopea* 9(1): 198–200. 2000. **Plate 22**.

Phymatarum differs from *Schismatoglottis* by its distinctly warty staminate flowers with the long-horned thecae, seeds with a long micropylar appendage, and basal placentation. It is an obligate rheophyte, but differs from all other such species by the long, creeping branching rhizome.

Taxonomy — World

One species endemic on Borneo.

Taxonomy — Borneo

See above.

Ecology

Obligate rheophyte on muddy or sandy river banks and eyots in lowland everwet broadleaf forest, occasionally becoming

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D. Inflorescence at onset of male anthesis, note the spathe limb caducous in a single piece and the pollen extruding in strings. **E.** Inflorescence at very late female anthesis. Note gaping orifice to the lower spathe. **F.** Spadix at early male anthesis with spathe artificially removed; **G.** Young infructescences showing the open orifice to the persistent lower spathe; the spathe limb in both examples have failed to fall after being shed due to dry air.

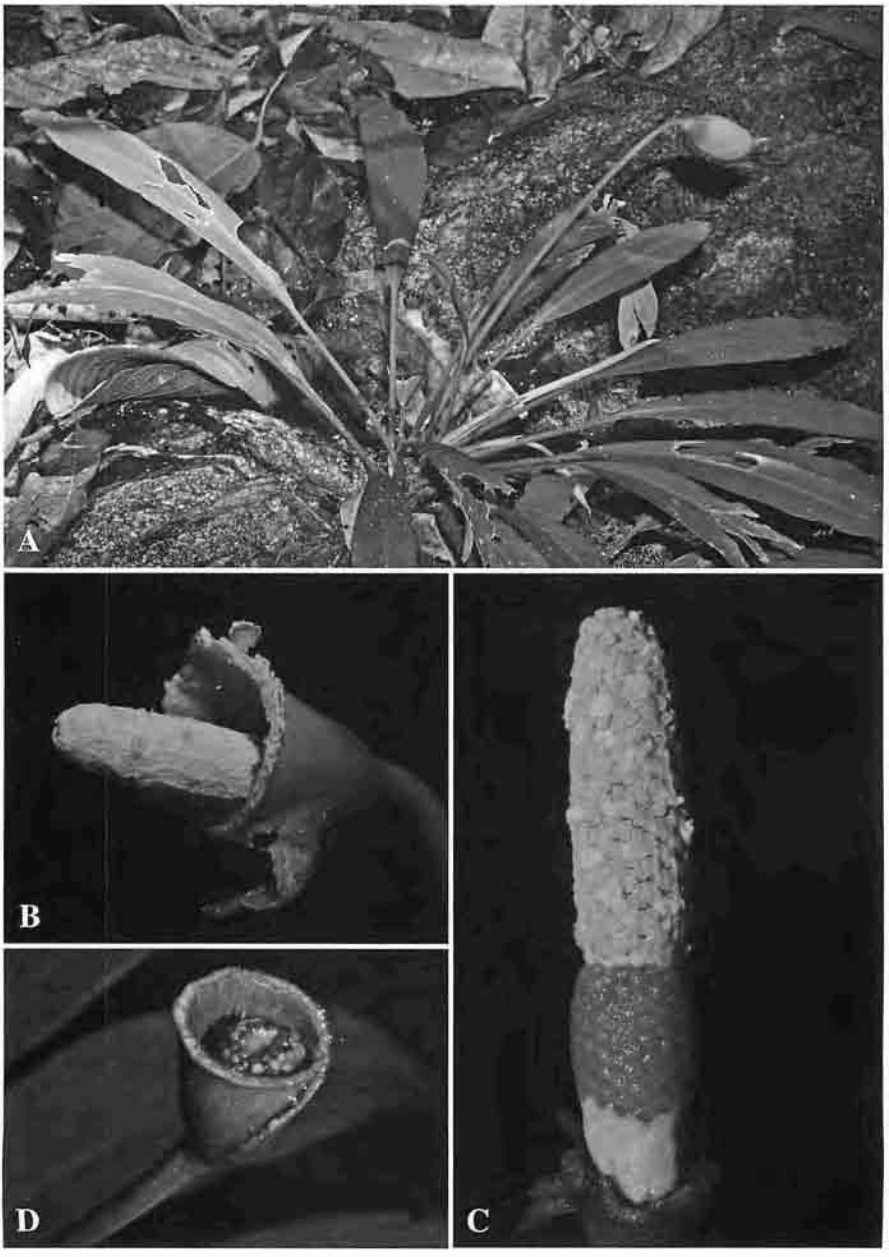

Plate 24. **Aroideae: Schismatoglottideae: *Piptospatha* N.E.Br. A–D:** *Piptospatha elongata* (Engl.) N.E.Br. **A.** Flowering plant in habitat on granite, Gunung Gading N.P., NW Sarawak. **B.** Inflorescence at onset of male anthesis. Note that the spathe limb has been shed to leave a cup-shaped persistent lower spathe. **C.** Inflorescence at male anthesis with spathe artificially removed to reveal spadix. **D.** Infructescence showing the persistent lower spathe and the fruits. Note that the upper part of the spadix has been shed (c.f. *Ooia*).

the dominant terrestrial herb species in logged-over areas and along margins of freshwater swamp forest.

Pichinia S.Y.Wong & P.C.Boyce, *Gardens' Bull. Sing.* 69(2): 297–304. 2010. **Plate 23.**

Pichina is one of two completely new genera of aroid discovered in Borneo in the past five years (the other being *Schottariella* P.C.Boyce & S.Y.Wong) as compared with several other novel genera erected as a result of better understanding of pre-existing genera (e.g. *Hestia*). It is perhaps indicative of the extraordinary wealth of Borneo's biodiversity that *both* wholly novel genera occur within a few hundred meters of human habitation in areas that are much utilized by local indigenous peoples for fishing and collecting forest produce.

Taxonomy — World

One species endemic on Borneo.

Taxonomy — Borneo

See above.

Ecology

Obligate lithophyte on Karst limestone blocks under everwet lowland evergreen broadleaf tropical forest.

Notes

The distichous arrangement appears to favor litter-trapping ability, the plants growing horizontally out from vertical or near-vertical surfaces. The leaf's common posture is with the lamina orthotropic to the petiole. Similar gross morphology and associated ecology is found in some *Homalomena* species, notably *H. punctulata* Engl.

Piptospatha N.E.Br., *Gard. Chron.*, n.s., 1879(1): 138 1879; Mayo, Bogner & Boyce, *Genera of Araceae* 184–187, Pl. 50, 117D. 1997; Bogner & Hay, *Telopea* 9(1): 201–218. 2000; Wong, Boyce & Bogner, *Gardens' Bull. Sing.* 61(1): 221–238. 2009; Wong & Boyce, *Bot. Stud. (Taipei)* in press. **Plate 24.**

Piptospatha is defined by the shedding spathe limb, erect splash cup, parietal placentation, fruits either fused into a syncarpium (most) or free but cohering (*P. insignis* N.E.Br.), and the presence of micropylar appendage on the seed. The pink, nodding inflorescences are diagnostic although similar inflorescences are found in *Ooia*.

Taxonomy — World

Eight species, two in West Malaysia and southern Thailand, six endemic on Borneo.

Taxonomy — Borneo

See above.

Ecology

Obligate rheophytes along streams and by waterfalls in lowland to lower montane perhumid to everwet tropical broadleaf forest. Several species are obligate to specific geologies, notably granite and limestone.

Notes

The characters used by Bogner & Hay (2000) to set generic boundaries were essentially those of Hotta (1965, 1966a,b, 1976), which outlined a genus having an inflorescence without a lower spathe/spathe limb constriction, seeds with micropylar appendages, staminate flowers lacking thecae horns, and a free ligular petiolar sheath. This generic circumscription was not supported by molecular phylogenetic study (Wong *et al.*, 2010) and resulted in the removal of several species into novel genera, *Bakoa* and *Ooia*.

Schismatoglottis Zoll. & Moritzi, *Syst. Verz.* 83. 1846; Mayo, Bogner & Boyce, *Genera of Araceae* 182–184, Pl. 49i–iii, 117C. 1997; Hay & Yuzammi, *Telopea* 9(1): 1–177. 2000; Hay, *Aroideana* 25: 67–69. 2002; Hay & Herscovitch, *Gar-*

Plate 25. **Aroideae: Schismatoglottideae: *Schismatoglottis* Zoll. & Moritzi. A–D:** *Schismatoglottis longispatha* W.Bull. **A.** & **B.** Plants in habitat showing two of the wide range of leaf markings encountered in a single populations. Plain green leaves also occur. **C.** Inflorescence at female anthesis. The spathe slightly inflating and gaping is typical of the

dens' Bull. Sing. 55: 27–30. 2003; Boyce & Wong, *Gardens' Bull. Sing.* 58(1): 7–18. 2006; Boyce & Wong, *Aroideana* 30: 56–70. 2007; Wong & Boyce, *Aroideana* 30: 71–81. 2007; Wong & Boyce, *Gardens' Bull. Sing.* 60(1): 155–163. 2008; Bogner & Boyce, *Gardens' Bull. Sing.* 60(2): 1–9. 2009. **Plates 25, 26**.

Schismatoglottis is defined by a constricted spathe, staminate flowers lacking thecae horns, seeds without a micropylar appendage, and parietal placentation. Growth ranges from stoloniferous, colonial helophytes to clumping or solitary rheophytes and lithophytes, with stems variously elongated and creeping to erect or even weakly climbing, to clumping and congested.

Taxonomy — World

In excess of 150 species, ranging from Sumatera to New Guinea and as far north as SW China, generally in wetter areas.

Taxonomy — Borneo

At least 100 species, virtually all endemic, many very locally so and often obligate to a specific geology, particularly limestone or shale.

Ecology

Terrestrial, often on steep slopes, lithophytic, rheophytic, or rarely chasmophytic in lowland to lower montane perhumid to everwet tropical evergreen forest.

Schottariella P.C.Boyce & S.Y.Wong, *Bot. Stud. (Taipei)*: 50: 269. 2009. **Plates 27, 28**.

The unique combination of morphologies displayed by *Schottariella* is smooth thecae with a hyaline ridge that becomes erect into a needle-like projection at the onset of male anthesis, an unconstricted spathe, a spadix frequently with distal pistillodes and seeds lacking a micropylar appendage and carried on a basal placenta. Basal placentation also occurs in *Piptospatha* but seeds of that genus also have a pronounced micropylar append age; *Piptospatha* differs from *Phymatarum* in having truncate stamens lacking a needle-like process.

Schottariella is remarkable for the needle-like structures, tipped with a weakly peltate ovate-triangular flap, emerging from the thecae (one per theca) only at the onset of male anthesis. Such a structure emerging in this manner is unique in the family—in all other species such thecae structures are present from well before the inflorescence opens and are not topped with flaps of any sort. The very slender nature of these needle-like structures recalls those of *Phymatarum* although in that genus the structures are present well before the onset of female anthesis; further the thecae of *Phymatarum* are notably verrucate (uniquely so in the tribe) while those of *Schottarum* are smooth. *Schottariella* shares basal placentation with *Phymatarum* but the ovules and seeds of *Schottariella* lack the characteristic micropylar appendage of *Phymatarum*.

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female phase spathe mechanics in *Schismatoglottis*. **D.** Inflorescence at female anthesis with spathe artificially removed. Points to note are the pistillate flower zone completely adnate to the decurrent spathe/spadix, the conspicuous zone of yellow staminodes between the pistillate and staminate flower zone, and the appendix also comprised of staminodes. **E–F**: *Schismatoglottis mayoana* Bogner & M.Hotta. **E.** Plants in habitat growing lithophytically. **F.** Detail of spadix at male anthesis. Note the pollen extruded in strings.

Plate 26. **Aroideae: Schismatoglottideae: *Schismatoglottis* Zoll. & Moritzi. A–D:** *Schismatoglottis corneri* A.Hay. **A.** Flowering plant in typical disturbed habitat. This individual is ca. 2m tall. **B.** Inflorescences. **C.** Inflorescence with portion of spathe artificially removed. Images © Kohei (Taekenaka) Takano.

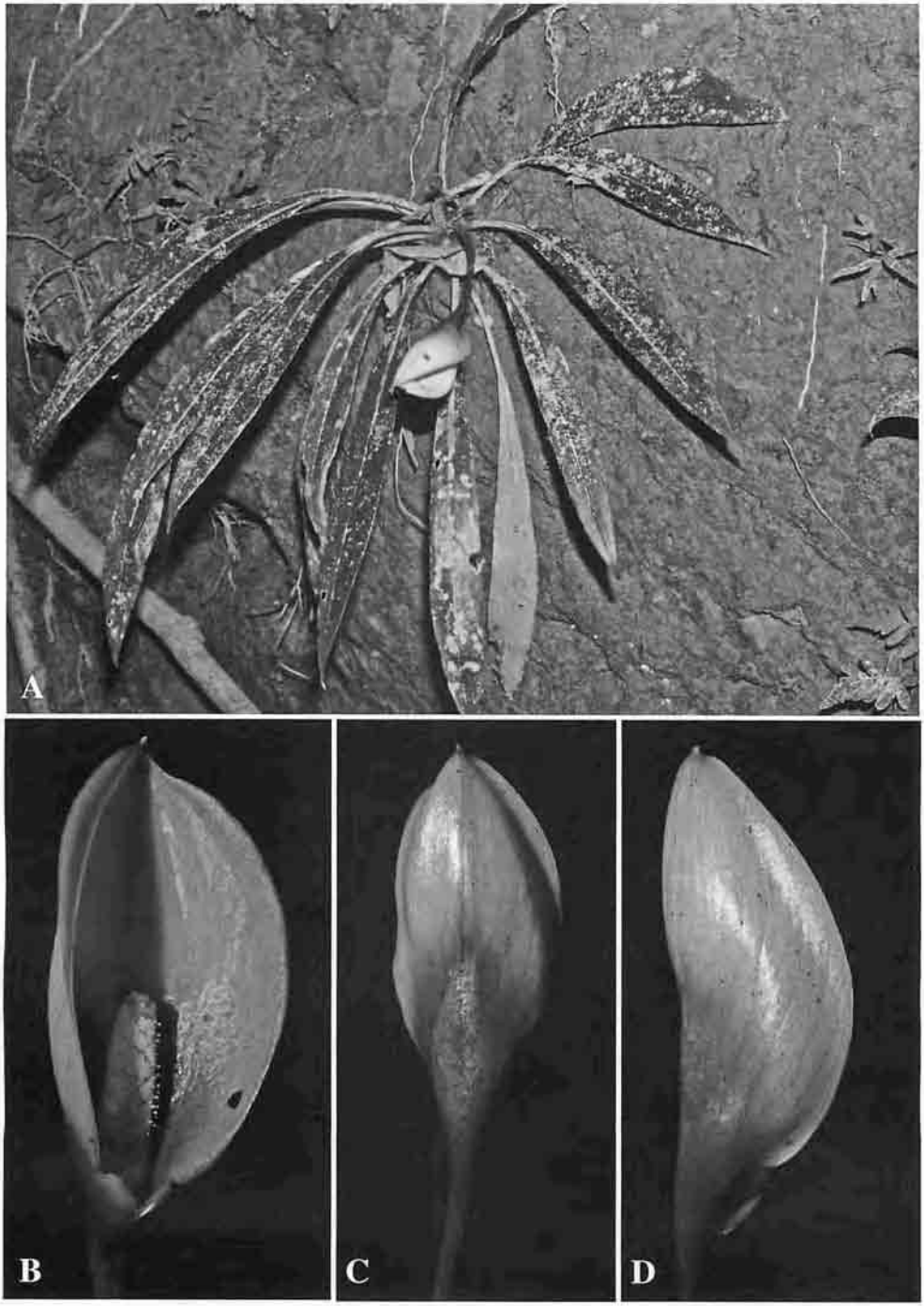

Plate 27. **Aroideae: Schismatoglottideae: *Schottariella* P.C.Boyce & S.Y.Wong. A–D:** *Schottariella mirifica* P.C.Boyce & S.Y.Wong. **A.** Plant in habitat on vertical clay river bank. **B.** Inflorescence at the onset of male anthesis with the thecae horns erect. **C.** Side view of spathe showing the strongly oblique lower spathe (green). **D.** Reverse view of spathe.

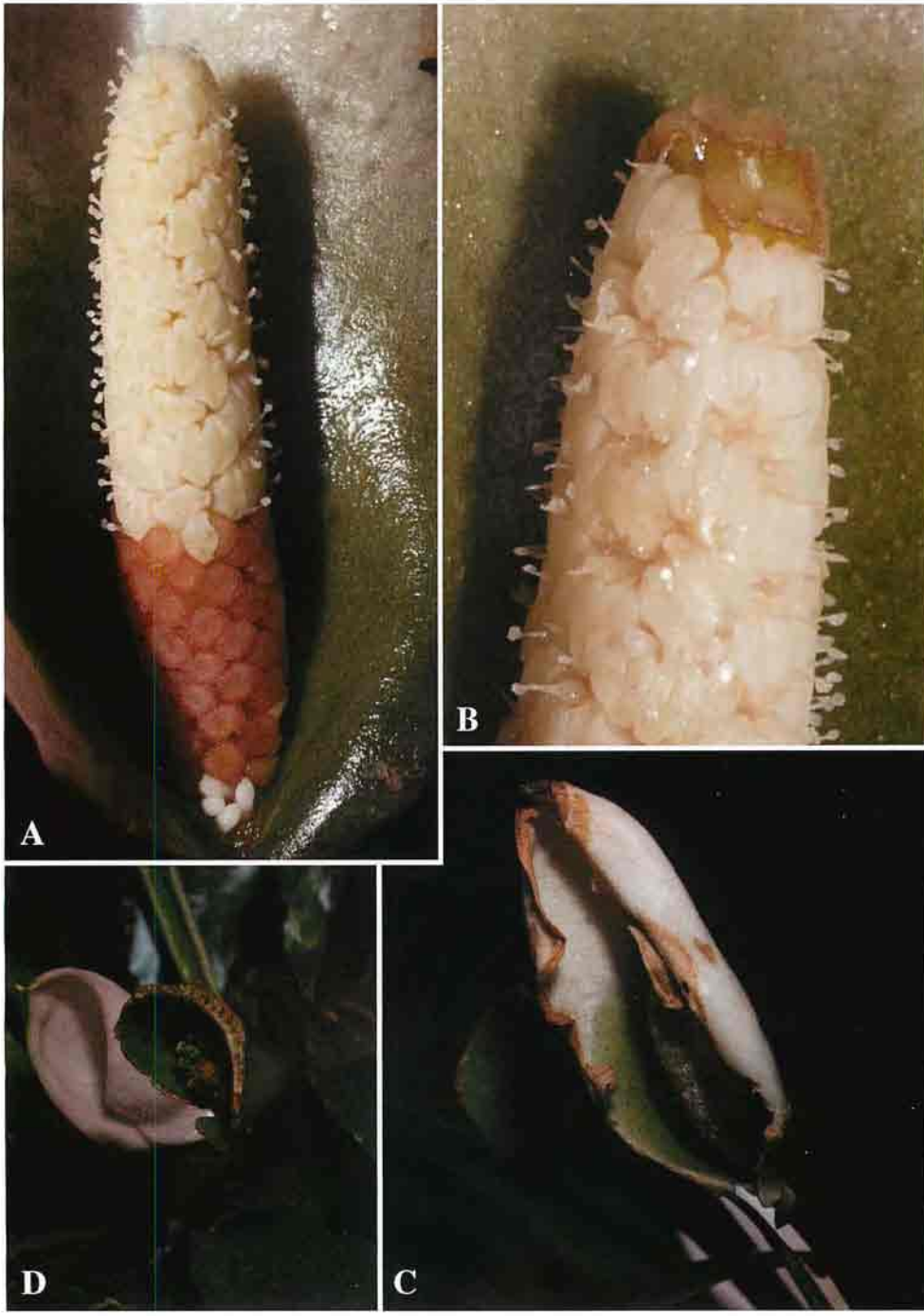

Plate 28. **Aroideae: Schismatoglottideae: *Schottariella* P.C.Boyce & S.Y.Wong. A–D:** *Schottariella mirifica* P.C.Boyce & S.Y.Wong. **A.** Inflorescence at male anthesis. Note the conspicuous thecae horns that have unfolded from the anthers. Note, too, the few white staminodes at the base of the pistillate flower zone. **B.** Detail of the spadix tip in a

Taxonomy — World

One species, endemic to Borneo.

Taxonomy — Borneo

See above.

Ecology

Old secondary and fragments of primary lowland riparian evergreen moist forest on shales. *Schottariella* is rheophytic on vertical clay-loam riverbanks.

Notes

The spadix with distal pistillodes in *Schottariella* is unique for the tribe; in all other Schismatoglottideae the terminal part of the spadix, an appendix, if present, is comprised of staminodes. We ascribe the distal organs as pistillodes based on observations of living plants where the highly distinctive pink pistils are clearly homologous with the structures forming the terminal part of the spadix and are quite different from the stipitate-clavate white staminodes associated with the pistils and the interstice between the staminate and pistillate flower zones.

Schottariella spathe limb senescence mechanics is unusual, although not unique, in the tribe by the spathe limb marcescent from the margins inwards and downwards and then, with the portion closest to the abscission layer still fresh, the spathe is shed. Similar (but probably not homologous) marginal marcescence occurs in the shoot-architecturally quite different *Schismatoglottis tecturata* (Schott) Engl. with only the margin marcescent and later shedding while the greater portion of the spathe is persistent, turning green and remaining more-or-less closed at the orifice and then shedding by abscission at the insertion of the peduncle by splitting and recurving basipetally at maturation of the fruits.

The spathe during fruiting of *Schottariella* is also peculiar in that while it is almost certainly a splash-cup, the margins of the persistent lower margins do not form a level rim but instead are obliquely declined towards the convolutions such that that the fruits/seeds are probably ejected forwards and away from the front of the cup rather than upwards and out as is known to be the instance in orthodox splash-cup dispersers, e.g. *Aridarum*. This view is further reinforced by the fruiting peduncle being arching/declinate thus presenting the lower spathe opening laterally or downwards rather than the peduncle being erect and the lower spathe held erect as is the situation in *Bucephalandra*, *Aridarum* and the *Piptospatha elongata* Group—all orthodox splash-cup dispersers.

Tribe Cryptocoryneae

Cryptocoryneae comprises two genera, *Cryptocoryne* Fisch. ex Wylder and *Lagenandra* Schott; the latter is absent from Borneo, being restricted to India, Bangladesh and Sri Lanka.

Cryptocoryne Fisch. ex Wydler, *Linnaea* 5: 428. 1830; Jacobsen, *Nordic J. Bot.* 5: 31–50. 1985; Mayo, Bogner & Boyce, *Genera of Araceae* 197–198, Pl. 57, 119B. 1997; Bastmeijer, *Aqua Pl.* 27(4): 145–146. 2002; Sasaki, *Aqua Pl.* 27(4): 147–149. 2002; Jacobsen, *Aqua Pl.* 27(4): 150–151. 2002; Jacobsen, Bastmeijer & Sasaki, *Aqua Pl.* 27(4): 152–154. 2002; Budianto & Basjmeijer, *Aqua Pl.* 29(4): 124–130. 2004; Wongso & Bastmeijer, *Aqua Pl.* 30(3): 92–100. 2005; Ipor, Tawan & Jacobsen, *Gardens' Bull. Sing.* 57: 1–6. 2005; Ipor,

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plant with a terminal appendix comprised of pistillodes. **C.** Inflorescence post anthesis with the spathe margins beginning to become marcescent prior to the spathe limb shedding along a strongly oblique line at the junction of the lower spathe. **D.** The distinctive oblique splash-cup of *Schottariella*.

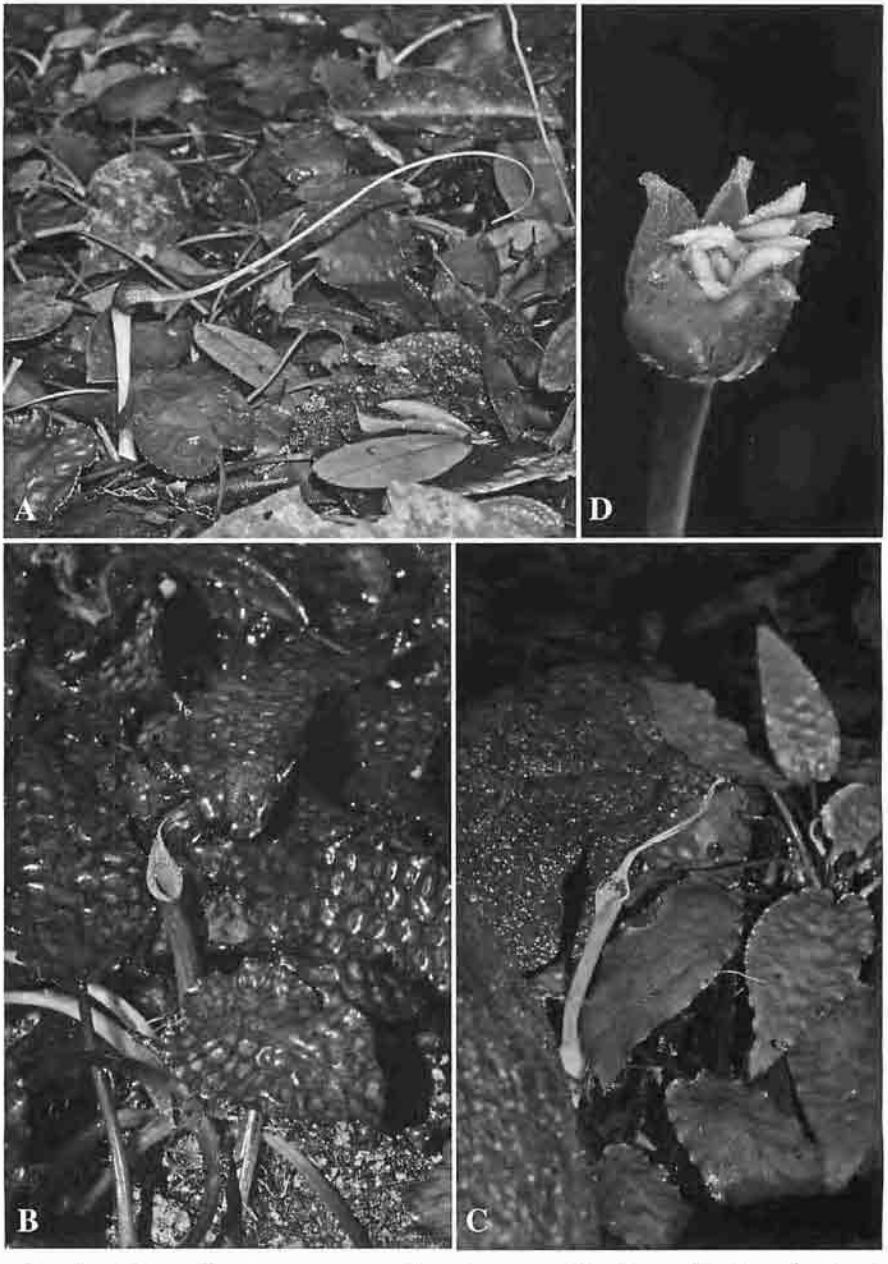

Plate 29. **Aroideae: Cryptocoryneae: *Cryptocoryne* Fisch. ex Wydler. A.** *Cryptocoryne longicauda* Engl., a distinctive species that is widespread in Sumatera, Peninsular Malaysia, and Borneo. **B.** *Cryptocoryne keei* N.Jacobsen, is restricted to a few localities in NW Sarawak. **C–D.** *Cryptocoryne striolata* Engl., a Bornean endemic, but there widespread. **C.** Flowering plant photographed in Mulu N.P., NE Sarawak, growing wedged between river stones and boulders. **D.** Ripe infructescence with the carpels open to release the seeds.

Tawan & Jacobsen, *Aqua Pl.* 31(2): 52–61. 2006; Ipor *et al.*, *Aqua Pl.* 32(3): 101–106. 2007 & 32(4): 131–140. 2007 & 33(1): 22–27. 2008 32(2): 48–52. 2008. **Plate 29**.

The inflorescence and fruits of *Cryptocoryne* are immediately diagnostic. The spathe comprises an inflated basal tube, the kettle, with united margins, an upper tube, sometimes twisted, with fused margins, and a terminal limb which opens into a flat, ovate surface that may either reflex, remain erect, when it may be spirally twisted, or arch forwards to form a hood and is usually terminated with a short to very long tail; a distinctive raised to callus-like collar is often found at the transition between the upper tube and limb. The fruits of *Cryptocoryne* are unusual in the family in being dehiscent, the individual carpels opening, with the fully open infructescence resembling a star.

Taxonomy — World

Perhaps 60 species occurring India and Sri Lanka through tropical Asia to New Guinea and northwards through Thailand and Indochina to SW China.

Taxonomy — Borneo

24 taxa, including 19 species, one nothospecies, three varieties, and one nothovariety of which 14 species, two varieties and one nothovariety are endemic.

Ecology

In Borneo *Cryptocoryne* are all aquatics (very rarely helophytes: *C. ciliata* (Roxb.) Fisch. ex Wylder) in freshwater or brackish streams in lowland to mid-elevation perhumid or everwet broadleaf forest. Only rarely do species occur in larger rivers in open habitats.

Notes

In recent years there has been, and continues to be, a great deal of attention directed towards the taxonomy and ecology of *Cryptocoryne* such that it is arguably the best understood aroid genus in tropical Asia. Nonetheless striking new species continue to be discovered.

Tribe Caladieae

Caladieae is in the main Neotropical, with only a single indigenous Asian genus, *Hapaline* Schott, although *Caladium* Vent., *Syngonium* Schott and *Xanthosoma* Schott are commonly cultivated, and not infrequently encountered as naturalized plants or weedy escapes. *Xanthosoma* is occasionally cultivated as a minor carbohydrate crop in Borneo.

Hapaline Schott, *Gen. Aroid.* 44. 1858; Bogner, *Pl. Syst. Evol.* 144: 59–66. 1984; Boyce, *Kew Bull.* 51(1): 63–82. 1996; Mayo, Bogner & Boyce, *Genera of Araceae* 216, Pl. 68, 121D. 1997; Boyce, Jeland & Jipom, *Gardens' Bull. Sing.* 57: 13–18. 2005; Boyce & Wong, *Gardens' Bull. Sing.* 60(1): 31–36. 2008. **Plate 30**.

Hapaline are diminutive to moderate-sized, slender to slightly robust tuberous or stoloniferous, clump-forming terrestrial, seasonally dormant or evergreen herbs with leaf laminae ranging from thin-textures to rather thick and leathery, and ranging in shape from ovate to hastate, with posterior lobes either present or absent, occasionally even in the same species. Leaf lamina variegation, in the form or irregular, often diffuse, silver-gray to pale green blotches occurs in many species.

Hapaline species all have white inflorescences, occasionally tinged green or grayish pink. Staminate flowers are fused into peltate synandria, with the synconnectives massively enlarged and with the thecae inserted on the lower margin of the connective tissue.

Taxonomy — World

Eight species ranging from Myanmar to China (Yunnan) and south through Thailand and Peninsular Malaysia to Brunei.

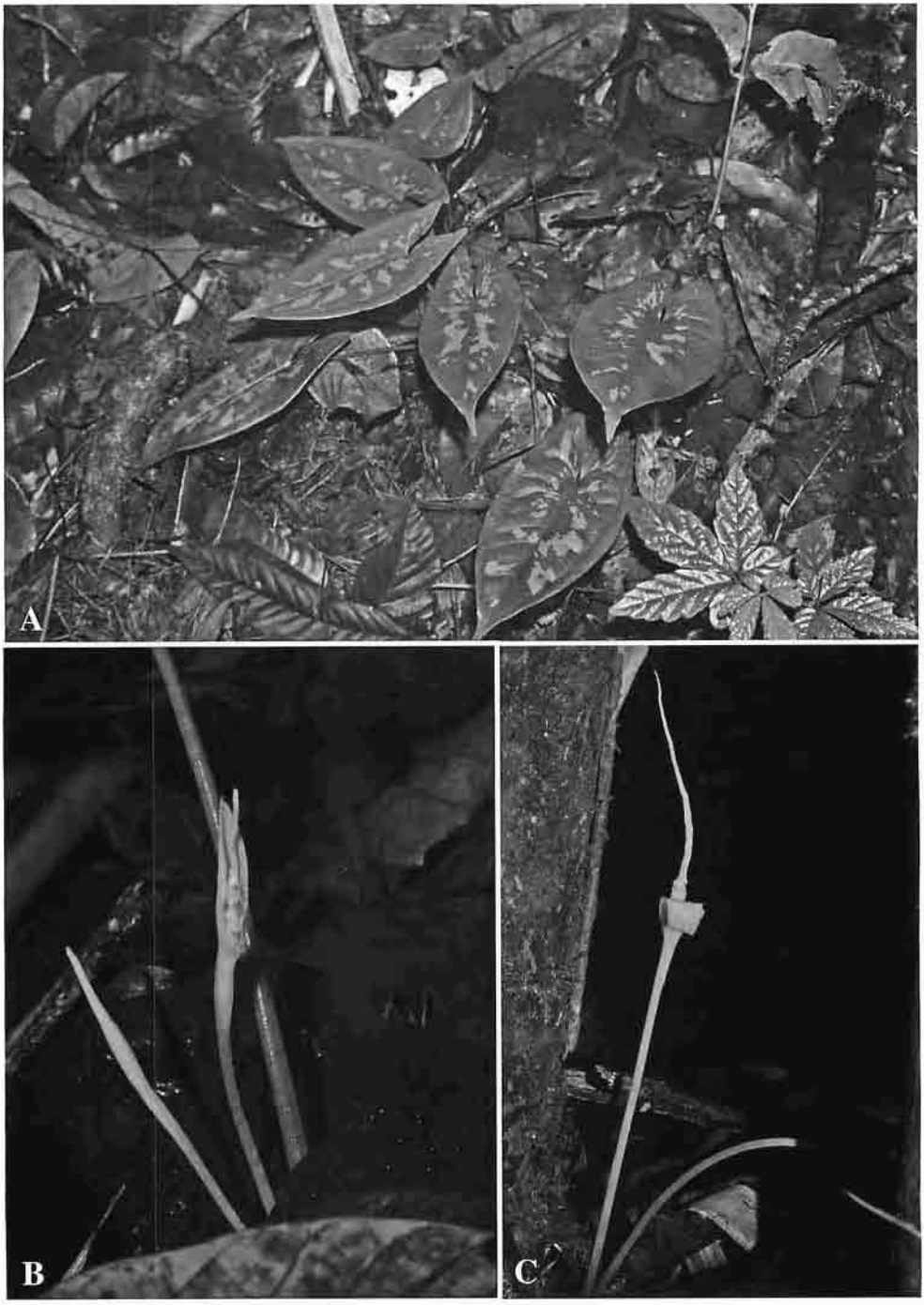

Plate 30. **Aroideae: Caladieae: *Hapaline* Schott. A–B:** *Hapaline celatrix* P.C.Boyce. Note the inflorescences carried well below the leaves and the short spadix appendix. **C.** *Hapaline appendiculata* Ridl. Note the diagnostic long spadix appendix.

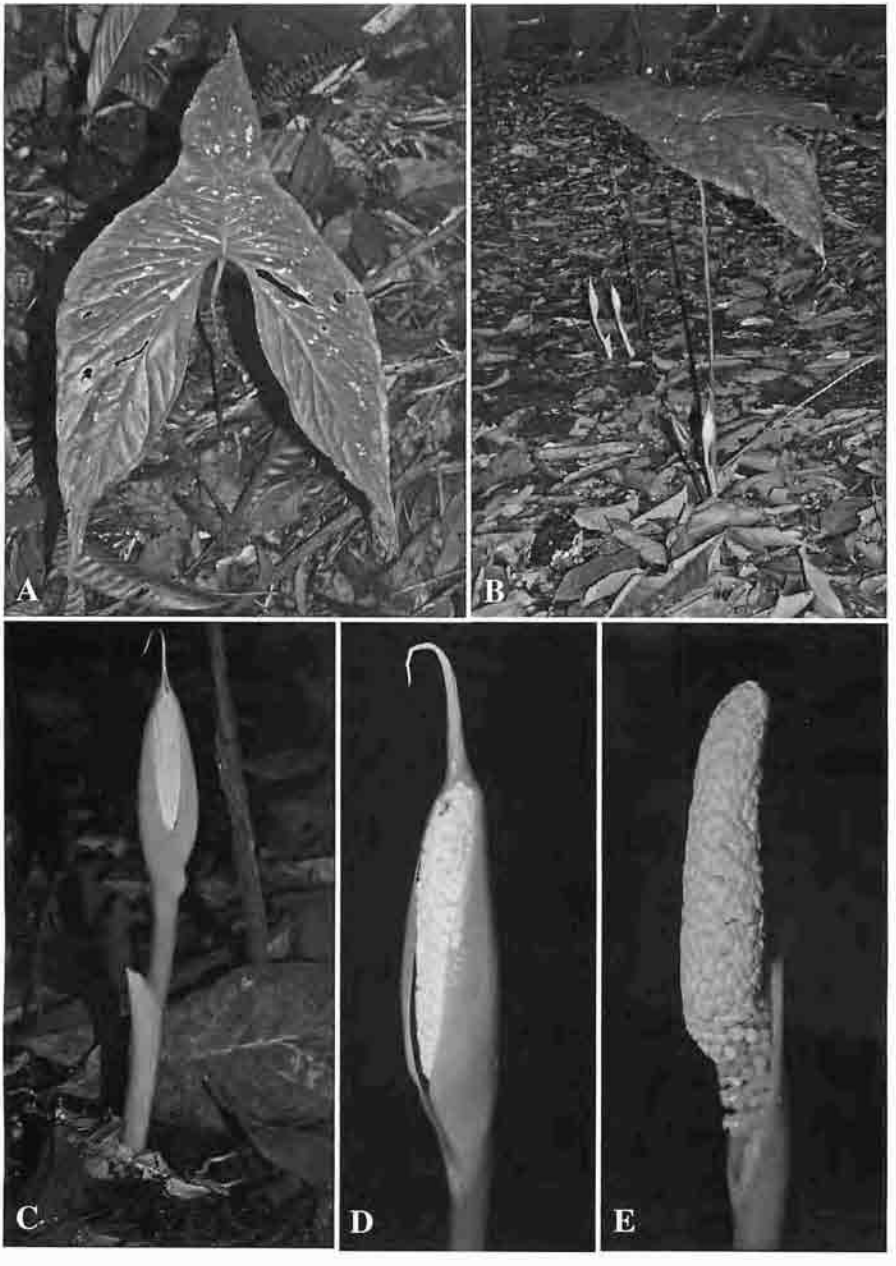

Plate 31. **Aroideae: Nephthytideae: *Nephthytis* Schott. A–E:** *Nephthytis bintuluensis* A.Hay, Bogner & P.C.Boyce. **A.** Plant in habitat. **B.** Flowering plants. Note that the leaves are far-scattered, and that the inflorescences also arise some distance in front of the associated leaf. The spathe turning green in the nearest plant is a developing infructescence. **C** & **D.** Inflorescence at female anthesis. Note that the spathe hardly opens. **E.** Inflorescence at female anthesis, spathe artificially removed. Note that the stamens do not form distinct floral groups.

Taxonomy — Borneo

Two species. Both endemic.

Ecology

Low to mid-elevation everwet, perhumid or seasonally dry broadleaf evergreen or deciduous forest (the last two not in Borneo). All species outside Borneo are limestone obligates whereas both Bornean species are shale-associated.

Notes

Hapaline in Borneo seems to be genuinely rare; the two known species occur as far-scattered small populations, with *H. appendiculata* Ridl. primarily confined to western and central Sarawak and *H. celatrix* P.C.Boyce to NE Sarawak and western Brunei.

Tribe Nephthytideae

The discovery in Borneo of an undescribed species of *Nephthytis*, a genus hitherto thought to be restricted to wet tropical west Africa, was, to say the least, unexpected. While many angiosperm genera extend through tropical Africa and Indomalesia [including *Rhaphidophora*, *Remusatia* Schott, *Sauromatum* Schott, *Arisaema* Bl., *Amorphophallus*, and *Pothos* (Madagascar) in the Araceae], Malesian-African tropical disjunctions were not known in aroids, and do not seem to be common generally.

Nephthytis Schott, *Oesterr. Bot. Wochenbl.* 7: 406. 1857; Hay, Bogner & Boyce, *Novon* 4(4): 365–368. 1994; Mayo, Bogner & Boyce, *Genera of Araceae* 216–218, Pl. 69, 122A. 1997. **Plate 31**.

Taxonomy — World

Six species with a disjunct distribution of five species in tropical West Africa and one species in NE Borneo.

Taxonomy — Borneo

One species. Endemic.

Ecology

Lowland riverine (alluvial-depositional) perhumid broadleaf evergreen tropical forest.

Notes

The leaf of *Nephthytis bintuluensis* A.Hay, Bogner & P.C.Boyce resembles that of *Cyrtosperma merkusii* and simple-leaved forms of *Lasia spinosa*. These are distinguished from *N. bintuluensis* by their armed petioles and clustered multiple leaves. See Hay, Bogner & Boyce, 1994.

Tribe Aglaonemateae

KEY TO THE GENERA OF BORNEAN AGLAONEMATEAE

1a. Colonial helophytes with creeping spongy rhizomes and erect, spongy petioles. Fruits large, ripening green and functioning as floating dispersal units . . . . . ***Aglaodorum***

1b. Terrestrial forest herbs with erect firm stems, and erect solid petioles. Fruits medium-sized, ripening red or rarely pink, not water dispersed. . . . . ***Aglaonema***

Aglaodorum Schott, *Gen. Aroid.*: 58. 1858; Mayo, Bogner & Boyce, *Genera of Araceae* 225, Pl. 78, 123A. 1997. **Plate 32**.

A single species closely allied to *Aglaonema*, *Aglaodorum griffithii* (Schott) Schott differs from *Aglaonema* in vegetative and fruit features seemingly associated with a swamp-dwelling habitat. Typically *Aglaodorum* occurs as a colonial helophyte in open swamps, especially on mud in freshwater and brackish tidal zones, usually in full sun. The stems and petioles are filled with air-spaces. The fruits, with very thick flesh, are green and evidently dispersed by floating. Unlike *Aglaonema* the petioles and peduncles are relatively long, elevating the leaf laminae and inflorescences above water.

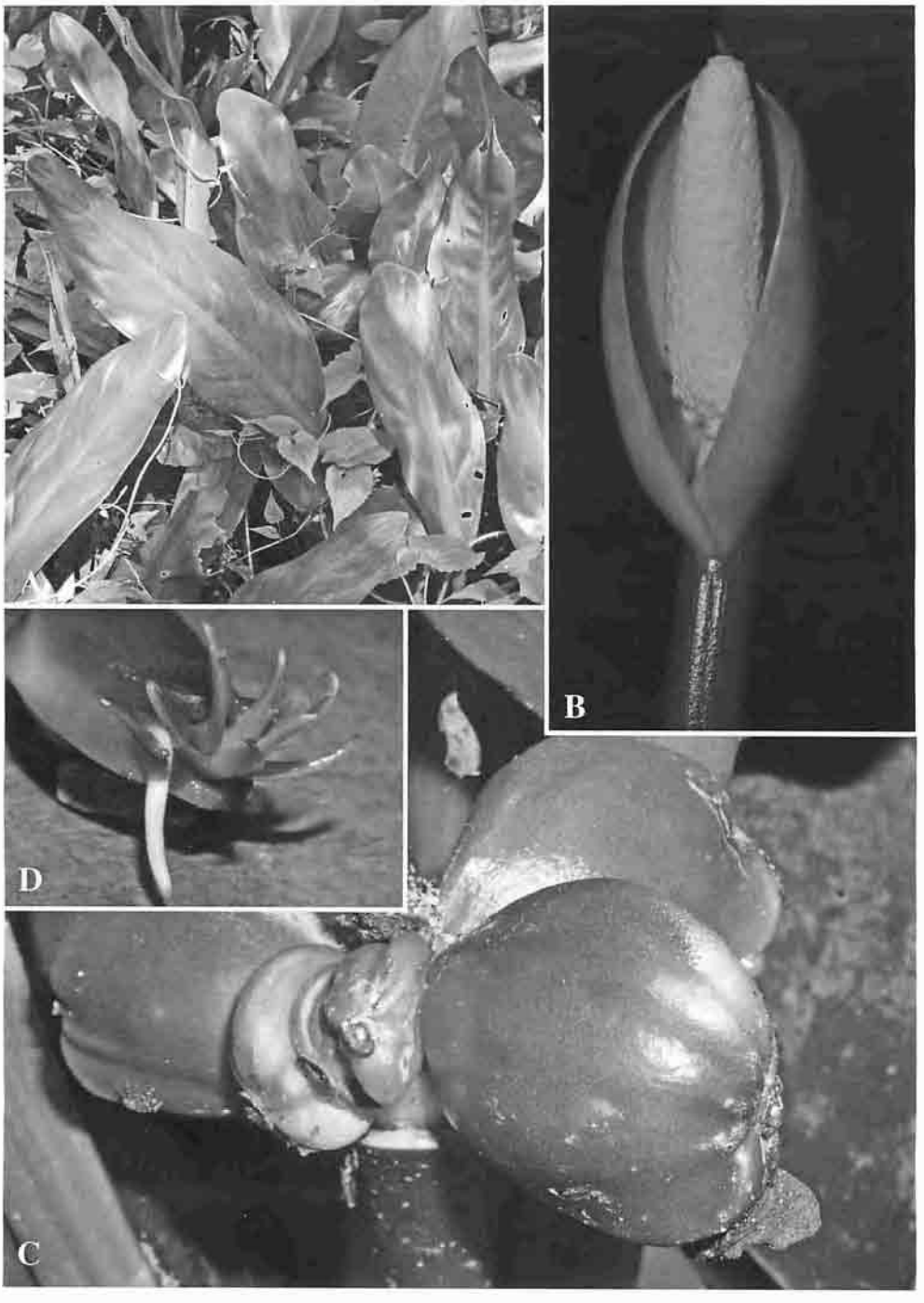

Plate 32. **Aroideae: Aglaonemateae: *Aglaodorum* Schott. A–E:** *Aglaodorum griffithii* (Schott) Schott. **A.** Plants in habitat. **B.** Inflorescence at female anthesis. **C.** Ripe infructescence. The large green fruits function as floating dispersal bodies. **D.** Germinating seed. Note that the fruit flesh has split to allow the emergence initially of the several hooked cataphylls. Only later does the root-radical emerge.

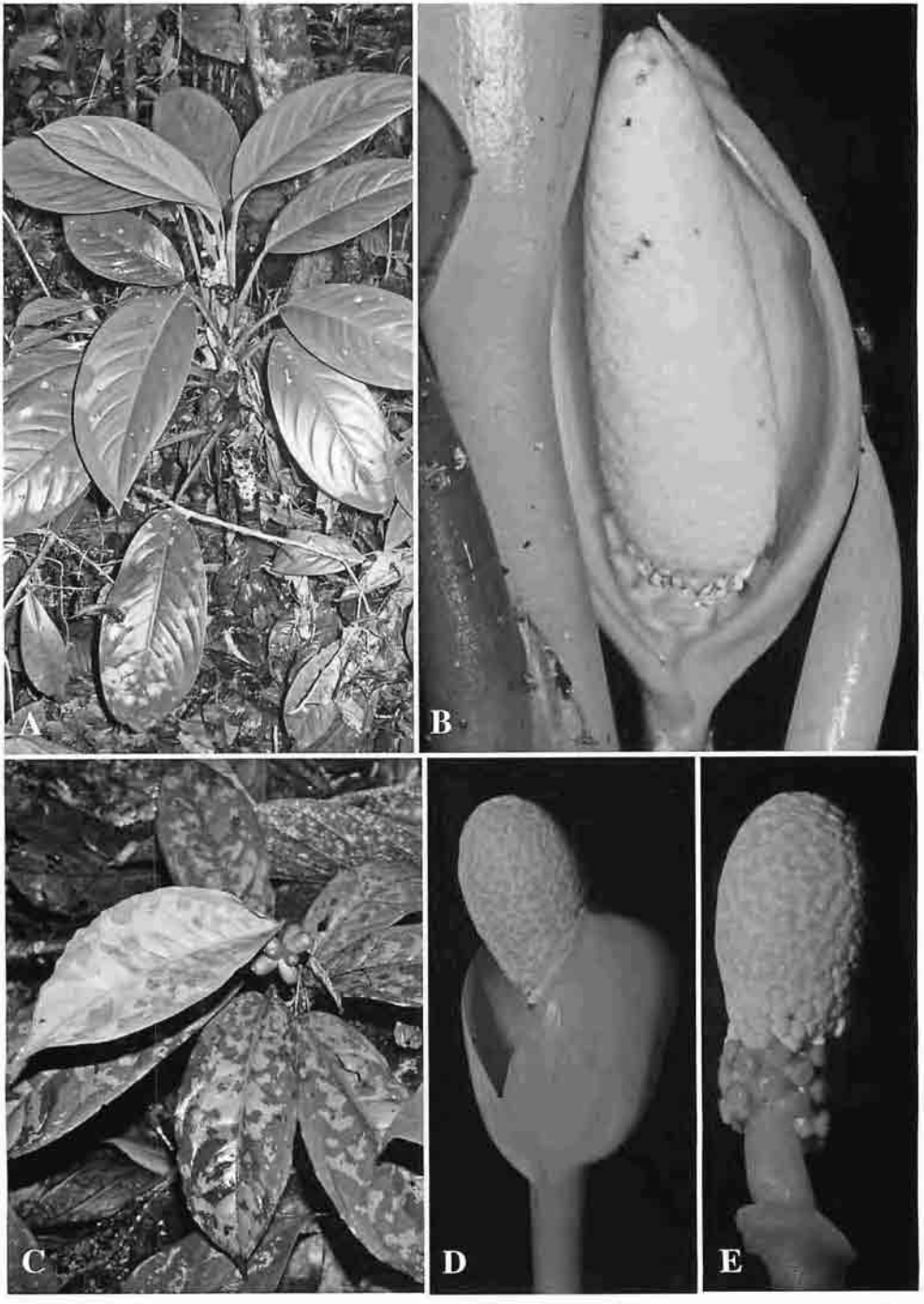

Plate 33. **Aroideae: Aglaonemateae: *Aglaonema* Schott. A–B:** *Aglaonema nitidum* (Jack) Kunth. **A.** Adult fruiting plant (over 1m tall). In some populations, as here, the fruits are ripe when pale pink, whereas mainly fruits ripen through to scarlet. **B.** Inflorescence at female anthesis. **C–E:** *Aglaonema nebulosum* N.E.Br. **C.** Fruiting plant in habitat.

Taxonomy — World

One species from southern Cambodia and Vietnam through Peninsular Malaysia and Sumatera to N. Borneo but seemingly absent from Sabah.

Taxonomy — Borneo

One species, not endemic.

Ecology

Colonial helophyte in tidal open swamps.

Notes

In Borneo *Aglaodorum* is often found between houses in stilt villages (*kampung air*) along tidal rivers.

Aglaonema Schott, *Wiener Z. Kunst* 1829: 892. 1829; Nicolson, *Smithsonian Contr. Bot.* 1: 1–69. 1969; Mayo, Bogner & Boyce, *Genera of Araceae* 223, Pl. 77, 122D. 1997. **Plate 33**.

Taxonomy — World

22 species in tropical and subtropical southeast Asia from northeastern India through to New Guinea.

Taxonomy — Borneo

Three species, none endemic.

Ecology

Primary and secondary perhumid to everwet broadleaf evergreen forests. A few species are restricted to kerangas or monsoonal perhumid semi-deciduous forests (the last not in Borneo).

Tribe Thomsonieae

Amorphophallus Blume ex Decne., *Nouv. Ann. Mus. Hist. Nat.* 3: 366. 1834, *nom. cons*; Mayo, Bogner & Boyce, *Genera of Araceae* 235–239, Pl.79 i–iv & 124C–D. 1997; Bogner, *Willdenowia* 18(2): 441–443. 1989; Bogner, Mayo & Sividasan, *Aroideana* 8: 14–25. 1985; Hetterscheid, *Blumea* 39: 237–281.1994. Hetterscheid & van der Ham, *Blumea* 46(2): 253–282. 2001; Boyce, Ipor & Hetterscheid, *Gardens' Bull. Sing.* 61(2):9–28. 2010. **Plate 34**.

Taxonomy — World

Over 200 species distributed from tropical Africa and Madagascar, throughout the Indian subcontinent, the subtropical eastern Himalayas, subtropical and tropical Asia into the tropical western Pacific and N.E. Australia.

Taxonomy — Borneo

At least 18 indigenous species, all endemic. One (*A. paeoniifolius* (Dennst.) Nicolson) almost certainly non-indigenous as found only in association with human disturbance; two further species' records (*A. prainii* Hook.f. and *A. konjac* K.Koch) require verification as Borneo is well outside their indigenous distributions.

Ecology

Lowland to upper hill forest perhumid to everwet broadleaf subtropical to tropical forest. Many of the Bornean species are locally endemic limestone obligates.

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Aglaonema nebulosum is restricted to *kerangas*. **D.** Inflorescence at female anthesis. Note the globose staminate portion greatly exceeds the spathe; this occurs at the onset of female anthesis and is enabled by a rapid extension of the spadix stipe. **E.** Inflorescence at female anthesis with the spathe artificially removed. Note the much-extended stipe.

Tribe Areae

In tropical Asia the Areae is a predominantly continental taxon, with the largest genus, *Typhonium* Schott, particularly species-rich and diverse in monsoonal Thailand and Indochina. The Areae is notable for the often elaborate sterile flowers separating the staminate and pistillate flower zones and the often strongly malodorous spadix appendix.

Typhonium Schott, *Wiener Z. Kunst* 3: 72. 1829; Mayo, Bogner & Boyce, *Genera of Araceae* 260–263, Pl.93 & 128A. 1997.

Taxonomy — World

Perhaps more than 100 species occurring from India through much of subtropical and tropical Asia into southern Japan. Species diversity is greatest in areas with strongly seasonal (wet-dry) climates. The Australian species hitherto included in *Typhonium* are currently the subject of molecular analyses.

Taxonomy — Borneo

Three species, non indigenous. See below.

Ecology

Occurring only in association with human habitation where their presence in all possibility is the result of introduction as medicinal plants.

Tribe Arisaemateae

Arisaema Mart. Flora 14(2): 459. 1831; Mayo, Bogner & Boyce, *Genera of Araceae* 270–275, Pl.98i–iv & 129A. 1997.

Arisaema is predominantly warm temperate Asian, with the greatest number of species and highest diversity occurring in China and Japan. The majority of *Arisaema* species are remarkable for their ability to change the sex of the inflorescences dependent on the size, maturity and overall vigor of the plant. Plants flowering for the first time, and weak mature individuals produce staminate inflorescences whereas robust plants in good health flower pistillate. This phenomenon is termed paradioecy.

Taxonomy — World

In excess of 200 species occurring from N America south to Mexico, E & NE Africa, the Arabian Gulf, through India to China and Japan and south through SE Asia to the Philippines.

Taxonomy — Borneo

4 species in Borneo, one (*A. umbrinum* Ridl.) endemic, but the genus in need of critical revision in the wet tropics

Ecology

Warm to cool temperate, subtropical or tropical dry, perhumid or everwet deciduous to evergreen broadleaf forest, rarely in warm temperate or subtropical coniferous woodland.

Tribe Colocasieae

Two genera of this large and important tribe occur in Borneo, *Colocasia* Schott and *Alocasia* (Schott) G.Don. The tribe features mostly large, sometimes gigantic erect to creeping herbs with milky to almost clear latex and often distinctly undulating interprimary collecting veins.

KEY TO THE GENERA OF BORNEAN COLOCASIEAE

1a. Infructescences erect, fruits medium-sized, ripening orange-red, odorless. . . . . ***Alocasia***

1b. Infructescences pendent, fruits small, ripening yellowish brown, smelling variously of overripe fruit or vomit . . . . . ***Colocasia***

Distinguishing *Alocasia* from *Colocasia*

Traditionally, these two genera, which are undoubtedly closely allied and frequently confused with one another, have been separated on the basis of ovule number and placentation—many ovules on parietal placentas in *Colocasia*, few on basal placentas in *Alocasia* (e.g. Mayo, Bogner & Boyce, 1997:90). These states are not really of practical use in field identification. However they translate in fruiting plants into markedly different dispersal syndromes, apparently (though not observed in West Malesia) involving birds in *Alocasia*, in marked contrast to the mammal dispersal syndrome of *Colocasia* where the fruits are smelly and inconspicuously colored with many tiny seeds in slimy mucilage (see Hay, 1996).

In respect of synflorescence architecture, *Alocasia* may be readily distinguished from *Colocasia* by its bimodular synflorescence subunits. Inflorescence multiplication in *Colocasia* is achieved in such a way that the whole synflorescence is equivalent to one bimodular unit in *Alocasia*. Where the inflorescence terminating the vegetative module has only one further inflorescence in the axil of its subtending cataphyll in *Alocasia* (with the synflorescence being built up by relay axes), in *Colocasia* the second inflorescence has a third in the axil of its prophyll and so on up to c. 8 in *Colocasia gigantea*. The relay axis in *Colocasia* is vegetative and thus the whole synflorescence is displaced to a quasi-lateral position on one side of the shoot.

Alocasia (Schott) G.Don, *Hort. Brit.*, ed. 3: 631. 1839, *nom. cons.*; Mayo, Bogner & Boyce, *Genera of Araceae* 283–286, Pl. 104i–ii & 130B. 1997; Hay, *Gardens' Bull. Sing.* 50: 221–334. 1998; Hay, *Bot. Mag., n.s.* 17(1): 14–18, pl. 381. 2000; Boyce, *Gardens' Bull. Sing.* 58(2): 141–154. 2007. **Plates 35, 36**.

Taxonomy — World

At least 100 species distributed from the subtropical eastern Himalayas throughout subtropical and tropical Asia into the tropical western pacific and eastern Australia.

Taxonomy — Borneo

41 indigenous species, of which 15 undescribed; 37 endemic, many locally so, and often restricted to specific geologies, particularly limestone, on which geology 16 species are obligate. One species (*A. macrorrhizos* (L.) G.Don) introduced as a carbohydrate crop and now widely feral.

Ecology

Primary and secondary perhumid to everwet subtropical and broadleaf tropical forests, open swamps; some species tolerant of quite strong seasonality; predominantly in the lowlands, extending from sea level to lower and mid-montane zones. Throughout its range *Alocasia macrorrhizos* is found only in association with human disturbance.

Colocasia Schott in H.W.Schott & S.L.Endlicher, *Melet. Bot.*18. 1832; Hay, *Sandakania* 7: 31–48 (1996); Mayo, Bogner & Boyce, *Genera of Araceae* 280–283, Pl. 103 & 130A. 1997. **Plate 37**.

Taxonomy — World

Probably fewer than 15 species distributed from the subtropical eastern Himalayas throughout subtropical and tropical Asia into the tropical western pacific and eastern Australia, with all of this distribution accounted for by *C. esculenta* (L.) Schott, a carbohydrate and less often green vegetable crop which is cultivated throughout the subtropics and tropics of both hemispheres.

Taxonomy — Borneo

Two species, one endemic.

Plate 34.

Plate 35.

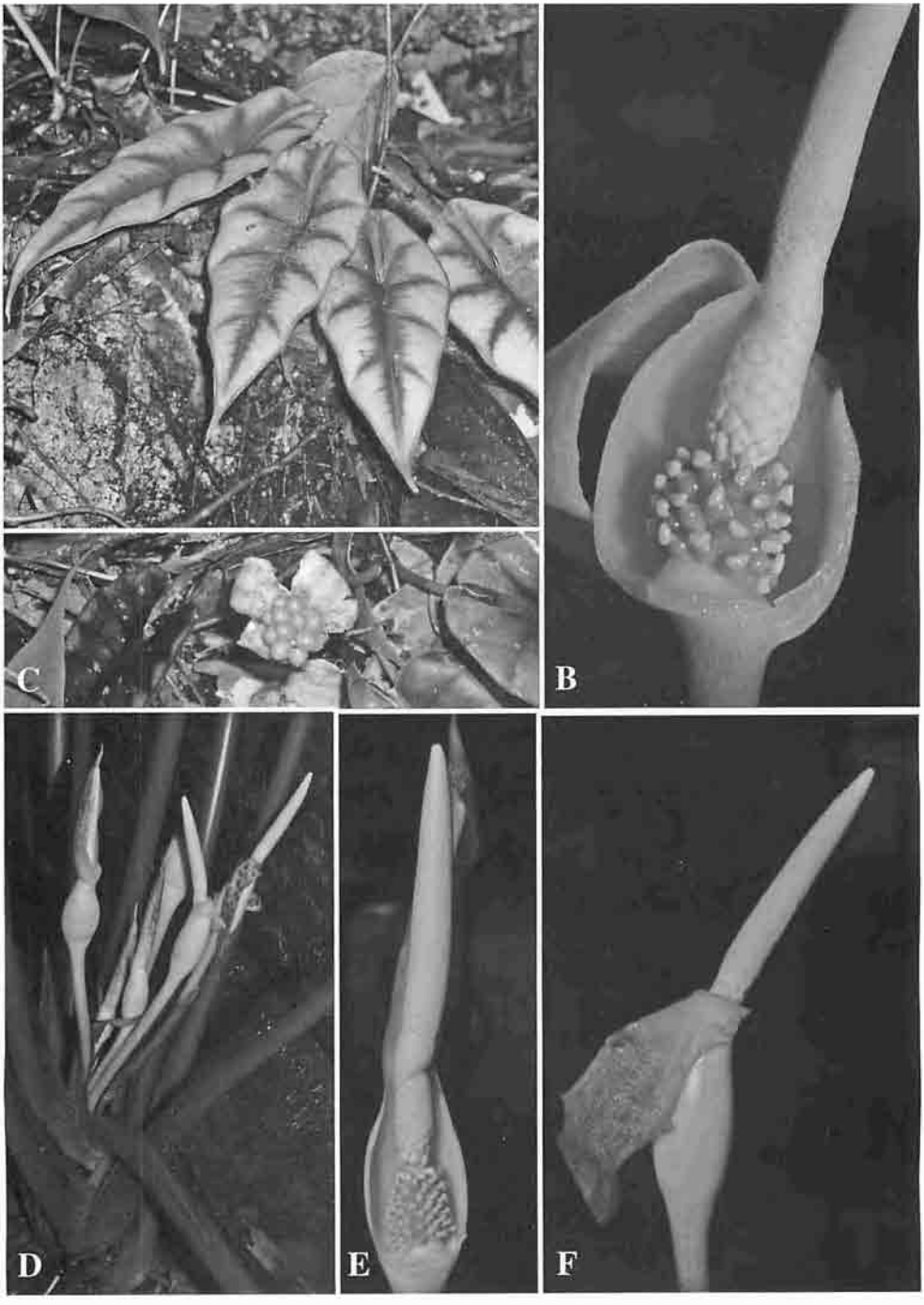

Plate 36.

Plate 34. **Aroideae: Thomsonieae: *Amorphophallus* Blume. A.** *Amorphophallus pendulus* Bogner & Mayo, remarkable for the greatly elongated spadix appendix. **B.** *Amorphophallus ranchanensis* Ipor, Tawan, A.Simon, Meekiong & Fuad, recently described from Permian limestone in south western Sarawak. **C.** *Amorphophallus julaihii* Ipor, Tawan & P.C.Boyce, endemic to the limestone rubble in Mulu N.P., from where it was described only in 2004. **D–E:** *Amorphophallus niahensis* P.C.Boyce, Ipor & Hett., known only from the Niah Caves N.P. in NE Sarawak, has just been described. It is one of several white-flowered species in Sarawak that, aside from spathe and spadix colouration, also share large ellipsoid fruits (**D**) and seeds.

Plate 35. **Aroideae: Colocasieae: *Alocasia* (Schott) G.Don. A–E:** *Alocasia longiloba* Miq. **A** & **B.** Variation in leaf markings and lamina shape. *Alocasia longiloba* is a highly variable species, notable for producing localized populations with highly distinctive morphologies but which, when viewed as part of the species as a whole co-exist with a range of intermediates. **C.** Inflorescences emerge from subtended by conspicuous prophylls and cataphylls in many populations (as here on Santubong, N Sarawak). **D.** Inflorescence at female anthesis with spathe partly removed. Note that constriction between the lower spathe and limb coincides with the sterile interstice separating the pistillate and staminate flower zones. Note, too, that the staminate flower zone is entirely outside the lower spathe. The conspicuously stellate stigma lobes are a feature of the Longiloba Group. **E.** Ripe infructescence. Note that the lower spathe has been shed some time before to leave a scar below the fruits. This is in contrast to other Bornean *Alocasia* in which the lower spathe persists until fruit maturity, at which point it actively splits downwards into strips that recurve to reveal the fruits (see Plate 36).

Plate 36. **Aroideae: Colocasieae: *Alocasia* (Schott) G.Don. A–C:** *Alocasia reversa* N.E.Br. **A.** Plants in habitat on Karst limestone, SW Sarawak. **B.** Inflorescence at female anthesis with spathe partly removed. Note that constriction between the lower spathe and limb does not coincide with the sterile interstice separating the pistillate and staminate flower zones but instead part way up the staminate flower zone, such that the staminate flower zone is partly entirely contained within the lower spathe. The Scabriuscula Group, to which *A. reversa* belongs have 2–3 lobed stigmas. **C.** Ripe infructescence, the persistent lower spathe has split into recurving pieces to reveal the ripe fruit. **D–F:** *Alocasia pangeran* A.Hay. **D.** Plant flowering in cultivation. The inflorescences are at different stages. That furthest left, with erect spathe limb, is at the female stage. That second from right, with the spathe limb reflexed and starting to decay is at late male anthesis. The inflorescence furthest right is post anthesis (spathe limb almost lost). **E.** Inflorescence at female anthesis with spathe partially removed. Note the erect spathe limb. Note, too, that the constriction between the lower spathe and spathe limb is rather weakly defined and coincides with a point ca. 1/3 along the staminate flower zone such that the majority of the staminate zone is enclosed in the lower spathe. **F.** Inflorescence at male anthesis. Note that the spathe limb is beginning to deliquesce prior to being shed.

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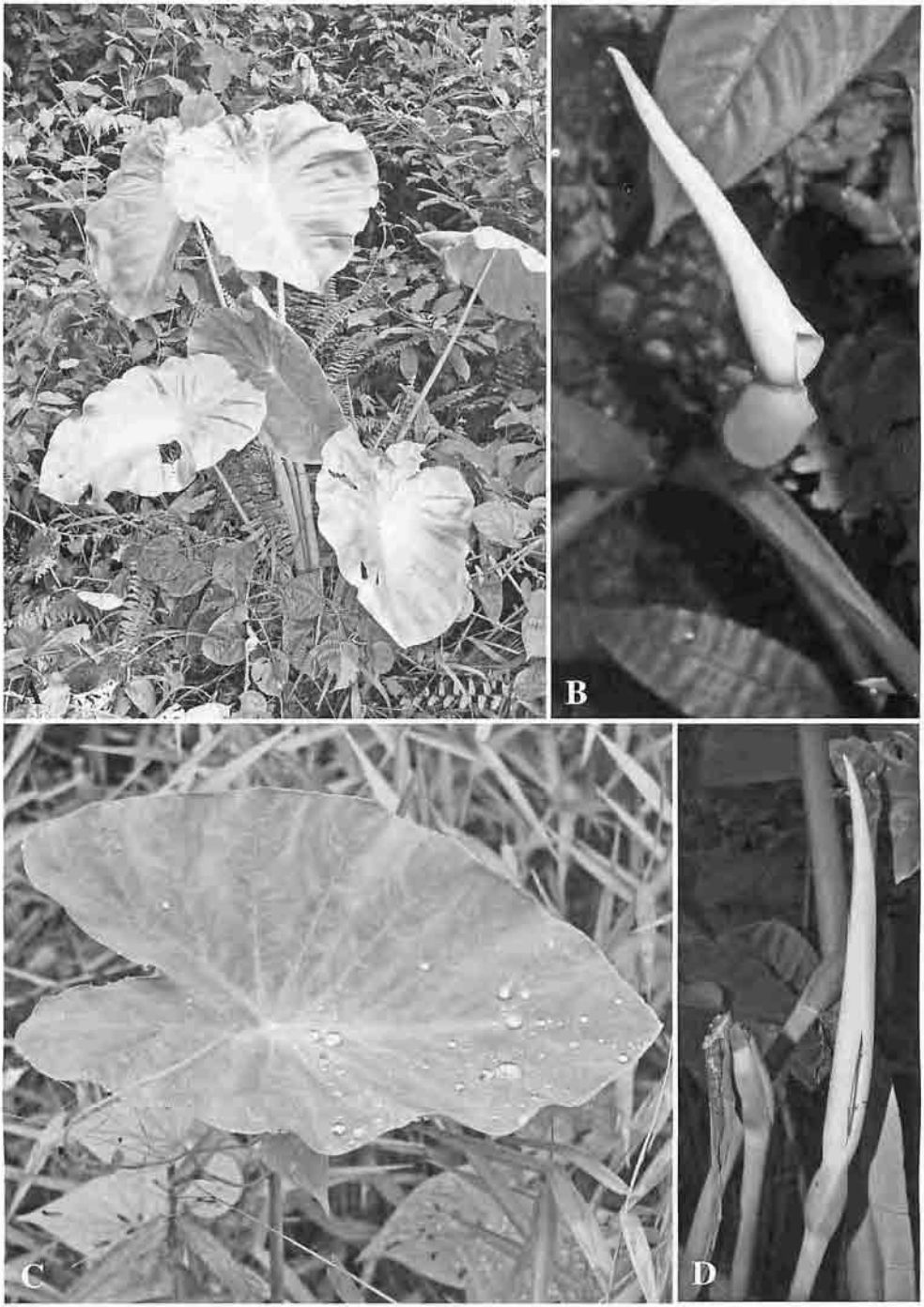

Plate 37. **Aroideae: Colocasieae: *Colocasia* Schott. A–B:** *Colocasia oresbia* A.Hay. **A.** Plants in habitat, Rejang. Note the glossy leaf lamina. **B.** Inflorescence at female anthesis. Note the proportionately shorter, stouter spathe limb. Note, too, the pale yellow-green color as compared with that of *Colocasia esculenta*. **C–D.** *Colocasia esculenta* (L.) Schott.

Ecology

Primary and secondary perhumid to everwet subtropical and broadleaf tropical forests, open swamps. *Colocasia esculenta* is predominantly in the lowlands, extending from sea level to lower and mid-montane zones whereas endemic *C. oresbia* A.Hay is confined to altitudes abouve 500m and is most abundant about 1,000 m. Throughout Borneo *C. esculenta* is found only in association with human disturbance.

Tribe Pisteae

Pistia L., *Sp. Pl.*: 963. 1753; Mayo, Bogner & Boyce, *Genera of Araceae* 286–288, Pl. 105 & 130C. 1997.

The ubiquitous water lettuce *Pistia stratiotes* L. is dubiously native to Borneo but frequently encountered.

Taxonomy — World

One species.

Taxonomy — Borneo

See above.

Ecology

Floating aquatic on slow moving or still water, often in roadside ditches and old monsoon drains.

ADVENTIVES

Four genera of exotic aroid (*Caladium* Vent., *Dieffenbachia* Schott, *Syngonium* Schott, and *Xanthosoma* Schott) are frequently encountered as adventives in Borneo. While usually close to habitation, on occasion exotic aroids (and, indeed other plants, notably species of Marantaceae, *Codiaeum*, *Dracaena* and even roses!) occur in areas of seemingly undisturbed forest, although an examination of the surrounding area will usually reveal activity related to collection of forest produce such as rattan, durian, etc.

Caladium is represented by *C.* × *hortulorum*, with large stands often occurring along the fringes of old rubber plantation and in fallow areas of oil palm plantation. Plants seldom flower and fruits have not been observed by any of the authors.

Dieffenbachia seguine (Jacq.) Schott is a popular ornamental plant in *kamungs* and long houses. Its decumbent-rooting habit and the brittle nature of the stems combined with the ability of even a small portion to regenerate means that it often forms large stands in sunny, wet places. Although flowering regularly, fruit set is exceedingly uncommon.

Syngonium podophyllum Schott is perhaps best regarded as semi-naturalized weed since it fruits prolifically and the fruits are dispersed by monkeys, squirrels, and various birds, notably bulbuls, and this combined with the plants' ability to vegetatively 'invade' stands of trees via creeping flagelliform shoots and also out-compete many local vining plants means that it often forms considerable areas of detrimental growth.

At least two *Xanthosoma* species occur as adventives close to longhouses, and appear to be the result of plants cultivated as carbohydrate crops escaping via the translocation of tuberules. *Xanthosoma* does not flower regularly in Sarawak, and none of the authors have ever witnessed fruits being developed.

In addition to the above species, numerous exotic aroids are cultivated in Borneo as ornamental plants. Among the Chinese community two aroids in particular, *Za-*

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C. Note the matte-glaucous leaf lamina and the manner in which the water-repelling wax forms water into discrete droplets. **D.** Inflorescence at female anthesis. Compare the proportionately longer, slimmer and rich-yellow spathe limb to that of *C. oresbia*.

mioculcas zamiifolia (Lodd.) Engl. and *Dieffenbachia paludicola* N. E. Br. ex Gleason, are widely favored as they are thought bestow good luck. The ability of *Zamioculcas* leaflets to fall, root, and produce a new plant is considered to bring both good fortune in terms of money and is also symbolic of rebirth—important in Buddhist and Taoist doctrines. *Dieffenbachia paludicola* is notable for the oblique position of the conspicuous leaf mid-rib, oblique to the left in some individuals, oblique to the right in others, and thus representative of the *ying* and *yang* of Taoist philosophy.

Other aroids variously popular in *kampungs* include various vining and self-heading *Philodendron* Schott, the ubiquitous *Epipremnum aureum* (Linden & André) G.S.Bunting, several *Aglaonema* species and hybrids, notably the very colorful Thai hybrids, *Caladium humboldtii* (Raf.) Schott, occasional plants of *Syngonium wendlandii* Schott and *S. macrophyllum* Engl. and *Spathiphyllum cannifolium* (Dryand. ex Sims) Schott.

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