

Studies on Schismatoglottideae (Araceae) of Borneo XXX — New species and combinations for Bucephalandra

Authors: Yeng, Wong Sin, and Boyce, Peter C.

Source: Willdenowia, 44(2) : 149-199

Published By: Botanic Garden and Botanical Museum Berlin (BGBM)

URL: <https://doi.org/10.3372/wi.44.44201>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

WONG SIN YENG^{1*} & PETER C. BOYCE²

Studies on *Schismatoglottideae* (Araceae) of Borneo XXX – New species and combinations for *Bucephalandra*

Abstract

Wong S. Y. & Boyce P. C.: Studies on *Schismatoglottideae* (Araceae) of Borneo XXX – New species and combinations for *Bucephalandra* – Willdenowia 44: 149–199. 2014. – Version of record first published online on 19 June 2014 ahead of inclusion in August 2014 issue; ISSN 1868-6397; © 2014 BGBM Berlin-Dahlem.

DOI: <http://dx.doi.org/10.3372/wi.44.44201>

Nineteen new species of *Bucephalandra* Schott are described: *B. akantha* S. Y. Wong & P. C. Boyce, sp. nov., *B. aurantiithecra* S. Y. Wong & P. C. Boyce, sp. nov., *B. belindae* S. Y. Wong & P. C. Boyce, sp. nov., *B. bogneri* S. Y. Wong & P. C. Boyce, sp. nov., *B. chimaera* S. Y. Wong & P. C. Boyce, sp. nov., *B. chrysokoupa* S. Y. Wong & P. C. Boyce, sp. nov., *B. diabolica* S. Y. Wong & P. C. Boyce, sp. nov., *B. forcipula* S. Y. Wong & P. C. Boyce, sp. nov., *B. goliath* S. Y. Wong & P. C. Boyce, sp. nov., *B. kerangas* S. Y. Wong & P. C. Boyce, sp. nov., *B. kishii* S. Y. Wong & P. C. Boyce, sp. nov., *B. minotaur* S. Y. Wong & P. C. Boyce, sp. nov., *B. oncophora* S. Y. Wong & P. C. Boyce, sp. nov., *B. pubes* S. Y. Wong & P. C. Boyce, sp. nov., *B. sordidula* S. Y. Wong & P. C. Boyce, sp. nov., *B. tetana* S. Y. Wong & P. C. Boyce, sp. nov., *B. ultramafica* S. Y. Wong & P. C. Boyce, sp. nov., *B. vespula* S. Y. Wong & P. C. Boyce, sp. nov. and *B. yengiae* P. C. Boyce, sp. nov. Furthermore, three pre-existing species names are transferred from *Microcasia* Becc. to *Bucephalandra*: *B. elliptica* (Engl.) S. Y. Wong & P. C. Boyce, comb. nov. (= *Microcasia elliptica* Engl.), *B. muluensis* (M. Hotta) S. Y. Wong & P. C. Boyce, comb. nov. (= *M. muluensis* M. Hotta) and *B. oblanceolata* (M. Hotta) S. Y. Wong & P. C. Boyce, comb. nov. (= *M. oblanceolata* M. Hotta). Together these changes take *Bucephalandra* to 27 species. An updated generic description is provided, and a key to all species is offered. All species dealt with taxonomically and nomenclaturally are illustrated from living plants, and with comparative plates of the spadices. Where possible scientific names are correlated to nomenclature used by commercial suppliers. Remaining taxonomic problems are highlighted, and foci for further study suggested. Notes on the role of the motile interstice staminodes are supplied.

Additional key words: aroids, aquarium plants, Malaysia, Sabah, Sarawak, Indonesia, Kalimantan, Brunei, taxonomy, identification key

Introduction

Studies of tribe *Schismatoglottideae* (sensu Wong & al. 2010) have made it evident that a significant proportion of the species are either undescribed or poorly circumscribed. Species-level taxonomy of *Bucephalandra* Schott in particular has been revealed to be much obfuscated by the difficulty of interpreting the abundant but mostly inadequately prepared herbarium specimens,

coupled with an almost complete failure to correlate the type material of the few published names to plants encountered in the field. It must be stated that this problem is by no means a new one; indeed it has been at the root of taxonomic confusion and misapplication of names in *Bucephalandra* ever since the genus was established by Schott in 1858. (Bogner 1980; Boyce & Wong 2012).

Over the past five years a significant living collection of *Schismatoglottideae* has been collected and main-

¹ Department of Plant Science & Environmental Ecology, Faculty of Resource Science & Technology, Universiti Malaysia Sarawak, 94300 Kota Samarahan, Sarawak, Malaysia; *e-mail: sywong@frst.unimas.my (author for correspondence).

² Honorary Research Fellow, Institute of Biodiversity and Environmental Conservation (IBEC), Universiti Malaysia Sarawak, 94300 Samarahan, Sarawak, Malaysia.

tained by the authors, and currently stands at c. 3000 accessions, of which c. 160 are *Bucephalandra*. All accessions are linked to precise locality and ecological data, and all plants that have flowered (the majority) have been vouchered and photographed. Liquid-preserved material and images are prepared whenever an accession flowers (not only on the first occasion) and by this means significant insight has been gained into inflorescence variation within each taxon. Observations of the more than 500 plants that the *Bucephalandra* accessions comprise have satisfied us that there exists a suite of reliable, although by no means always easy to observe, floral and vegetative morphological characteristics that coupled with precise geographical and ecological data provide a reliable basis for the new taxa we are proposing.

We are anticipating some negative reaction to the significant increase in the number of species proposed here, especially since the current standard revision (Bogner & Hay 2000) takes a conservative view on species delimitation. In justification of our species' concepts, aside from the morphological distinctions used, as we progressed on this paper and continue to work on the large number of plants that we have yet to identify, it has become clear that a factor in the richness of aroid (and doubtless other) species in Borneo is a high prevalence of geological specialization. In verifying geological occurrences for this paper we have been much assisted by the excellent geological map of Tate (2001).

This is the first of a series of papers working toward a monograph of *Bucephalandra*. We estimate that the genus *Bucephalandra* probably consists of more than fifty species.

Foci for further study

Numerous areas of *Bucephalandra* taxonomy remain poorly understood. From the viewpoint of taxonomic stability the most pressing need is the recollection of the generic type, *B. motleyana* Schott, not seen in the wild since James Motley's original gathering in what is today Kalimantan Selatan. Motley's type locality remains imprecise, although based on Motley's known activities it is probably in the S part of the Meratus Mountains, which even then (the 1850s) were within relatively easy travelling of Banjarmasin, the closest large city and port. Commercial names applicable to as yet undetermined species in the *Bucephalandra* Motleyana Complex are: 'Amanda', 'Brownie', 'Diana', 'Helena', 'Neoamanda', 'Themis' and 'Ulysses'.

The *Bucephalandra* Pygmaea Complex also presents considerable problems, despite the recent recollection of *B. pygmaea* (Becc.) P. C. Boyce & S. Y. Wong (Boyce & Wong 2012). To date, we are only able to resolve four species: *B. pygmaea*, *B. diabolica* S. Y. Wong & P. C. Boyce, sp. nov., *B. sordidula* S. Y. Wong & P. C. Boyce, sp. nov. and *B. tetana* S. Y. Wong & P. C. Boyce, sp. nov. Many of the numerous *Bucephalandra* being offered commercial-

ly fall into this complex, and most are very likely undescribed. Commercial names applicable to as yet undetermined species belonging to the *Bucephalandra* Pygmaea Complex are: 'Aurora', 'Biblis', 'Biblis Pink', 'Black Centipede', 'Cascade', 'Centipede', 'Cherish', 'Claudia', 'Copper Leaf', 'Cypris', 'Emerald Carpet', 'Ghost', 'Hyperion', 'Melawi', 'Midnight Blue', 'Perfect Ghost', 'Shine Blue', 'Silver Powder', 'Stay Unique Stay Foolish', 'Theia' and 'Theia Blue'.

Note on dimensions

Dimensions used in the descriptions are derived from fertile (i.e. mature) plants. Seedlings will have overall smaller measurements.

Results and Discussion

Bucephalandra Schott, Gen. Aroid.: t. 56. 1858; Prodr. Syst. Aroid.: 319. 1860; Engl., Monogr. Phan. 2: 354. 1879; Nat. Pflanzenfam. 2(3): 132. 1889; Pflanzenr. 55 (IV.23Da): 122. 1912; Bogner in Aroideana 3: 134–143, fig. 1–15. 1980; & in Pl. Syst. Evol. 145: 159–164. 1984; Boyce in Bot. Mag. 12: 131–134, pl. 272. 1995; Boyce & al. in Bot. Mag. 12: 150–153. 1995; Mayo & al., Gen. Araceae: 189, pl. 52. 1997; Bogner & Hay in Telopea 9: 195–198. 2000; Boyce & Wong in Webbia 67: 139–146. 2012. – Type: *Bucephalandra motleyana* Schott. = *Microcasia* Becc. in Bull. Reale Soc. Tosc. Ort. 4: 180, fig. 8. 1879; Engl., Monogr. Phan. 2: 299. 1879; & in Beccari, Malesia 1: 290, t. 22, fig. 21–24 & t. 25, fig. 2–8. 1883; N. E. Br., Gen. Pl. 3(2): 986. 1883; Engl., Nat. Pflanzenfam. 2(3): 132, fig. 85. 1889; Ridl. in J. Straits Branch Roy. Asiat. Soc. 44: 183. 1905; Engl., Pflanzenr. 55 (IV.23Da): 128, fig. 77. 1912; Hotta in Mem. Coll. Sci. Univ. Kyoto, Ser. B, 32: 20–22, fig. 1. 1965. – Type: *Microcasia pygmaea* Becc. (= *Bucephalandra pygmaea* (Becc.) P. C. Boyce & S. Y. Wong).

Description — Minute to rather large evergreen, obligate (very seldom facultative) rheophytic herbs. *Stem* creeping and rooting, with active apex upright, or erect, or stems rooted at base with remainder pendent and active tips ascending. *Leaves* mostly numerous; *petiole* shorter, equalling, or longer than leaf blade, often with conspicuous longitudinal ridges; *petiolar sheath* with a long marcescent ligule; *blade* elliptic, elliptic-oblong, linear-oblan-ceolate or obovate, stiffly coriaceous to membranous, often punctate abaxially, rarely so adaxially, apex mostly with a tubular mucro; *primary lateral veins* pinnate, adaxially flush with blade to prominently raised, abaxially ± flush with blade, running into variously distinct marginal vein; *interprimary veins* parallel-pinnate; *higher order venation* either parallel-pinnate or reticulate, or tessellate, usually very faint. *Inflorescence* solitary, or a few in sequence with each separated by a conspicuous prophyll

or less often a foliage leaf; *peduncle* sub-equalling to much-exceeding petiole at anthesis, rarely (*Bucephalandra gigantea*) much shorter, always elongating later, often longitudinally keeled. *Spathe* ellipsoid to lanceolate, cuspidate, not constricted; *lower spathe* broadly funnel-form at and post-anthesis, persistent into fruiting, later subtending and enclosing developing fruits, light green to yellow or reddish, convolute; *limb* white, pink, or yellow, gaping at pistillate anthesis, variously senescing and then caducous at onset or during staminate anthesis. *Spadix* sessile or very briefly stipitate, shorter than spathe, usually with a few *pistillodes* at extreme base; *pistillate zone* cylindric to obconic, mostly narrower than upper parts, with pistils in 2–8 spirals; *pistils* mainly depressed globose or depressed trapezoidal, 1-locular; *ovules* many, orthotropous, attenuate toward micropyle, funicle distinct, placenta basal; *stigma* sessile, discoid, umbonate to slightly concave in centre, narrower than ovary; sterile interstice a few rows (usually 2, sometimes as many as 5 or as few as 1) of flattened, smooth, *scale-like motile staminodes*, these erect at pistillate anthesis, deflexing prior to staminate anthesis to seal lower spathe, turning green and persisting into fruiting; *staminate zone* with 2–9 rows of stamens; flowers unistaminate; *filament* usually distinct but very short, flattened, connective either inconspicuous or most often expanded as an extension of filament into a flattened triangular-cordate or spatulate structure with thecae on ventral surface of distal arms; *thecae* ellipsoid to globose, extrorse, dehiscing by a pore at tip of a short to long conspicuous apical horn; *pollen* extruded in a droplet, inaperturate, ellipsoid, medium-sized (range 28–30 μm long; Grayum 1992: 21), exine psilate. *Appendix* globose or ellipsoid to (sub-)cylindric, or bullet-shaped, composed of columnar to obpyramidal irregular polygonal to rounded apically papillose, echinate, smooth, or brain-like *staminodes*, uppermost often \pm connate, less often appendix entirely comprised of connate staminodes. *Fruit* a globose to ellipsoid berry with numerous seeds, protected until maturity by persistent interstice staminodes; *seed* narrow-ellipsoid, with long, curved micropylar appendage, testa very slightly longitudinally ribbed to scabrous; embryo straight, elongate; endosperm copious.

Ecology — Obligate, very seldom facultative, rheophytes on stream and riverside rocks in lowland to lower montane perhumid to moist tropical forest.

Distribution — *Bucephalandra* is endemic on Borneo, with most species locally so, and seemingly always associated with a specific geology. It is also becoming apparent that at least some species are attitudinally obligate.

Etymology — From Greek, *bous* (bull or cow), *cephalē* (head) and *anēr, andros* (man), in reference to the shape of the individual staminate flowers.

1. *Bucephalandra akantha* S. Y. Wong & P. C. Boyce, **sp. nov.** — Fig. 1, 23A & 25.

Holotype: Malaysian Borneo, Sarawak, Bahagian Kuching, Padawan, Annah Rais, Kampung Sadir, Air Terjun Sadir, 01°06'28.3"N, 110°16'47.1"E, 6 Apr 2012, P. C. Boyce & al. AR-3863 (SAR!; isotypes: SBC!, SING!).

Diagnosis — *Bucephalandra akantha* is distinguished from all other species with papillate appendix staminodes by the staminate flowers with divergent, sharply angled thecae and stout, stiff thecae horns.

Description — Small, rather robust obligate rheophytic herbs to c. 17 cm tall, occurring mainly as individual plants, only occasionally in small patches. *Stem* creeping, branching repeatedly, branches 0.5–6 cm long \times 2–4 mm in diam., rooting with active portions bright reddish purple, sub-erect. *Leaves* arching, to c. 10 together; *petiole* c. 4 cm long \times c. 2 mm in diam., adaxially strongly canaliculate, deep reddish, sheathing at extreme base, wings extended into a very narrowly triangular ligular portion to 1 cm long; *blade* elliptic, 8–10 cm long \times 2–2.5 cm wide, coriaceous, semi-glossy dark green adaxially, tinged reddish pink abaxially, base cuneate, apex rounded and apiculate for c. 1.5 mm, margin somewhat undulate; *midrib* adaxially prominent, abaxially prominent and reddish; *primary lateral veins* 3 or 4 on each side, diverging at 25°–60° and running to a marginal vein; *interprimary veins* alternating with primaries, almost of equal width; *secondary venation* adaxially \pm obscure. *Inflorescence* solitary; *peduncle* sub-equalling to somewhat exceeding petioles, 3–5 cm long, conspicuously longitudinally sulcate and distally winged, bright reddish purple, this colour derived from multitudinous, minute speckles. *Spathe* broadly ovate, not constricted, c. 2.5 cm long; *lower spathe* funnel-form, pale green, persistent; *limb* inflating and gaping distally at pistillate anthesis, caducous during late staminate anthesis, glistening white, apiculate for c. 3 mm, apiculum pale green. *Spadix* 1–1.5 cm long, very shortly stipitate; *stipe* less than 0.5 mm long, longitudinally sulcate, glossy white; *pistillate zone* 2.5–3 mm long \times c. 2 mm in diam., with c. 3 spirals of pistils; *pistils* cylindric-globose, c. 0.5 mm in diam., pale lime-green; *stigma* sessile, umbonate, c. $\frac{3}{4}$ diameter of ovary, papillate at anthesis, later (post-anthesis) sunken centrally; *pistillodes* in a single incomplete row at base of pistillate zone, squat fusiform with a terminal beak, in all c. 0.35 mm in diam., c. $\frac{1}{2}$ as wide, glossy white; *interstice* with 1–3 rows of *scale-like staminodes*, these 1–2 mm long \times 0.8–1.5 mm wide, margin slightly thickened, staminodes initially erect (pistillate anthesis), then during staminate anthesis reflexing until perpendicular with spadix axis, with tips somewhat ascending, initially greenish white, later (post-anthesis) becoming green and persisting to cover developing fruit; *staminate zone* c. 5 mm long \times 2–3 mm in diam., consisting of 4 or 5 rows of flowers; *staminate flowers* pale to medium yel-

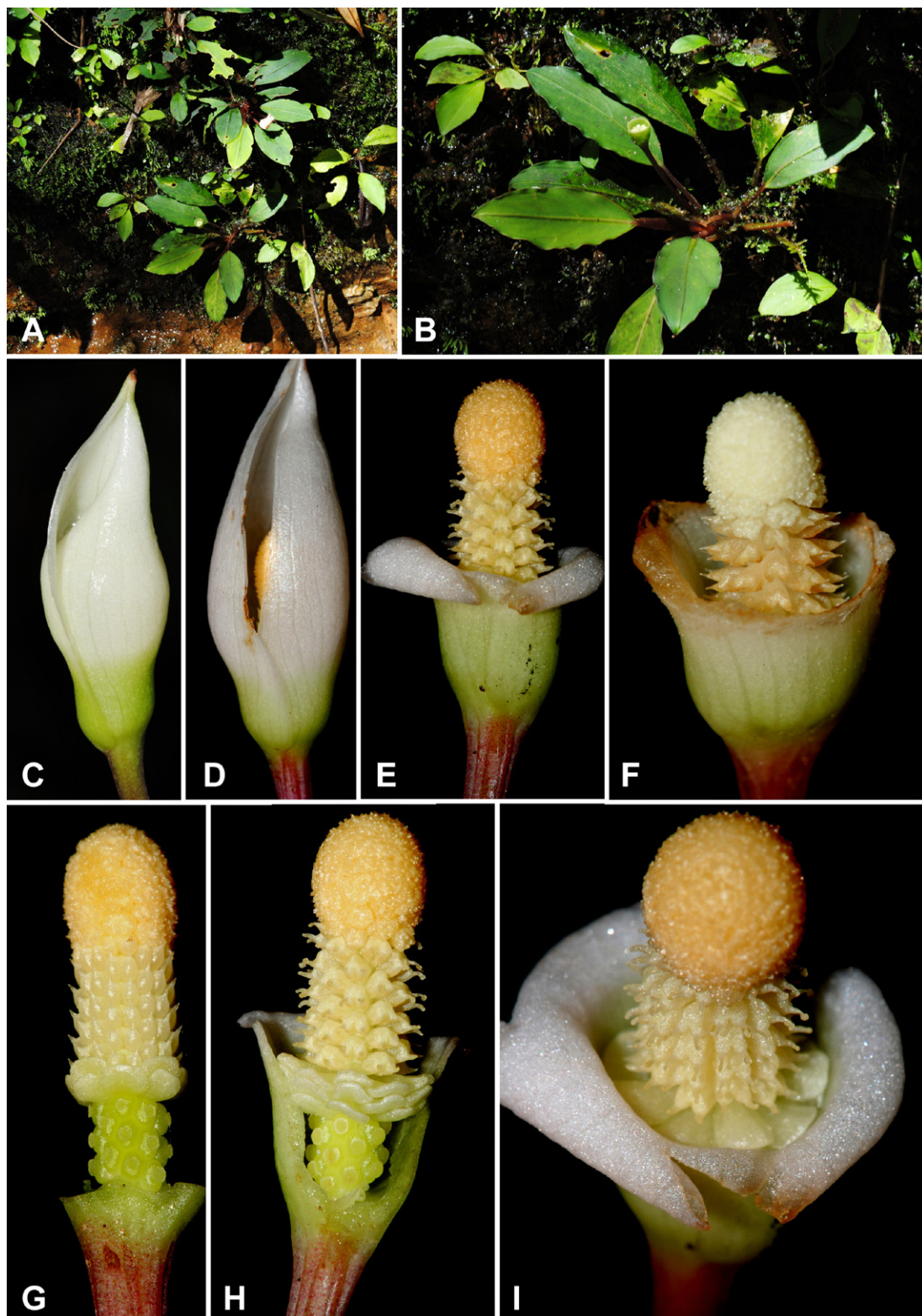


Fig. 1. *Bucephalandra akantha* – A & B: plants in habitat; C & D: inflorescence at early pistillate anthesis; E: inflorescence at staminate anthesis; most of spathe limb has been shed, with remaining portion reflexed; persistent lower spathe is still somewhat narrow; note, too, pollen droplet secreted at tip of staminate flower theca horn; F: inflorescence post-staminate-anthesis; remaining portion of spathe limb has been lost, and persistent lower spathe has expanded laterally; G: spadix at pistillate anthesis, spathe artificially removed; note that interstice staminodes are still erect and staminate flower thecae have yet to reflex; H: spadix at staminate anthesis, spathe limb fallen naturally, nearside of lower spathe artificially removed; interstice staminodes have reflexed to seal lower spathe entrance, and thecae of staminate flowers have reflexed and produced pollen droplets from tips of horns; I: inflorescence during staminate anthesis, with reflexed interstice staminodes clearly visible blocking entrance of persistent lower spathe. – Photographs: A, B & F from P. C. Boyce & S. Y. Wong AR-3863; C–E, G–I from K. Nakamoto AR-3884; all by P. C. Boyce.

low; *stamen* comparatively large, c. 1 mm across, cream; *filament* short but conspicuous; *connective* strap-shaped; *thecae* inserted lateral-ventrally on connective, individually ellipsoid, c. 1 mm long × c. 0.4 mm wide, smooth; *thecae horns* c. ½ length of associated theca, stiffly setaceous, with bases somewhat swollen, spreading to slightly downward-directed during pistillate anthesis, upward-pointing during staminate anthesis; *appendix* ± globose, c. 4 mm long × c. 3 mm in diam., dark cream to medium yellow; *appendix staminodes* mostly obpyramidal (although lowermost ones transitioning in appearance to staminate flowers), densely arranged, 0.5–1 mm in diam., tops strongly echinate. *Fruiting spathe* funnel-form, c. 1 cm in diam., medium green, with green shield-shaped staminodes persistent and spent distal part of spadix falling; *berry* depressed globose, 1–1.8 mm long × 1–1.5 mm in diam., medium green, with numerous seeds, berries forming a hemispherical cluster protected by persistent staminodes, later pushed off and falling to reveal mature fruits; *fruits* decomposing at maturity, forming a pulp with seeds held in persistent lower spathe; *seeds* narrowly ellipsoid, 1–2 mm long × 0.25–0.3 mm in diam., light brown, very slightly longitudinally ribbed, with a curved micropylar appendage to 1 mm long.

Ecology — *Bucephalandra akantha* occurs on granite and metamorphosed sandstone riverside rocks under per-humid lowland forest at between 100–200 m above sea level.

Distribution — NW Borneo: Padawan and Siburan districts (Sarawak: Bahagian Kuching) and Kecamatan Entikong (Kalimantan Barat: Kabupaten Sanggau).

Etymology — Greek noun, *akantha* (thorn), in reference to the thorn-like appearance of the staminate flowers.

Remarks — In the N part of its range (Sarawak) *Bucephalandra akantha* occurs allopatrically W of the alkaline-geology-obligate *B. bogneri*.

Commercial names — None.

Additional specimens seen (paratypes) — INDONESIA BORNEO: KALIMANTAN BARAT: Kabupaten Sanggau, Kecamatan Entikong, SW of Entikong, 10 Apr 2012, K. Nakamoto AR-3884 & AR-3889 (BO!, SAR!); Kecamatan Entikong, 10 km W of Sanggau, 10 Apr 2012, K. Nakamoto AR-3888 (BO!, SAR!).

2. *Bucephalandra aurantiitheca* S. Y. Wong & P. C. Boyce, **sp. nov.** – Fig. 2 & 23B.

Holotype: Indonesian Borneo, Kalimantan Barat, Kabupaten Sekadau, Kecamatan Nanga Taman, SE of Manterahidup, 00°08'45.2"S, 111°00'47.0"E, 22 May 2012, K. Nakamoto AR-3937 (BO!; isotypes: SAR!, SBC!, SING!).

Diagnosis — *Bucephalandra aurantiitheca* is one of two *Bucephalandra* species with conspicuous orange thecae; the other is the sympatric *B. chimaera*, from which *B. aurantiitheca* is distinguished by the staminate flowers arching upward from the spadix and by very short downward-directed thecae horns.

Description — Small obligate rheophytic herbs c. 18 cm tall. *Stem* erect, occasionally somewhat decumbent and rooting with active portion sub-erect, c. 1 cm in diam. *Leaves* many together, erect-arching; *petiole* 6–9 cm long × c. 2 mm in diam., weakly carinate, very deep red, sheathing at extreme base, wings extended into a narrowly triangular ligular portion c. 3 cm long; *blade* lanceolate-elliptic, sometimes slightly oblique and/or weakly falcate, 7–9 cm long × 1.5–2 cm wide, coriaceous, semi-glossy dark green adaxially, pale yellow green abaxially, base sub-cuneate, apex acuminate and apiculate for c. 3 mm, margin undulate; *midrib* abaxially prominent, red, adaxially slightly raised; *primary lateral veins* c. 4 on each side, diverging at c. 30° and running to a rather conspicuous marginal vein; *interprimary veins* alternating with primaries, very much finer but darker than blade; *secondary venation* adaxially obscure, abaxially forming a faint reticulate pattern; *tertiary venation* obscure. *Inflorescence* solitary, or up to three together separated by prophylls; *peduncle* exceeding petioles, 5–7 cm long × c. 2 mm in diam. (on average), longitudinally sulcate, pale green with numerous bright reddish speckles, these particularly concentrated in sulcae, giving peduncle a candy-striped appearance. *Spathe* oblong-ovate, not constricted, 4–5 cm long; *lower spathe* initially narrowly funnel-form, later (staminate anthesis) flaring, medium semi-glossy green, persistent; *limb* slightly inflating and gaping distally at pistillate anthesis, opening widely almost to persistent lower spathe during staminate anthesis, caducous during late or post-staminate anthesis, with margins recurving, and limb often retaining a slender connection to lower spathe, ivory, acuminate for c. 4 mm and apiculate for c. 1.5 mm, apiculus dull orange. *Spadix* 2.5–3 cm long; *pistillate zone* sessile, c. ½ width of remainder of spadix; 3–5 mm long × c. 3 mm in diam., with 3–5 spirals of pistils; *pistils* very closely appressed, rhombic-cylindric, c. 0.5 mm in diam., pale creamy yellow; *stigma* sessile, button-like, c. ½ diameter of ovary, papillate at anthesis; *pistillodes* absent; *interstice* with 1–3 somewhat incomplete rows of *scale-like staminodes*, these c. 2 mm long × 1.8 mm wide, margin thickened, staminodes initially erect (pistillate anthesis), then during staminate anthesis reflexing until sub-perpendicular with spadix axis, with body of staminode depressed and tips ascending, initially greenish white, later (post-anthesis) becoming green and persisting to cover developing fruit; *staminate zone* 6–8 mm long × c. 6 mm in diam., consisting of 3–5 rows of flowers; *staminate flowers* cream; *stamen* comparatively large, c. 1 mm tall, c. 0.7 mm wide; *filament* very short;

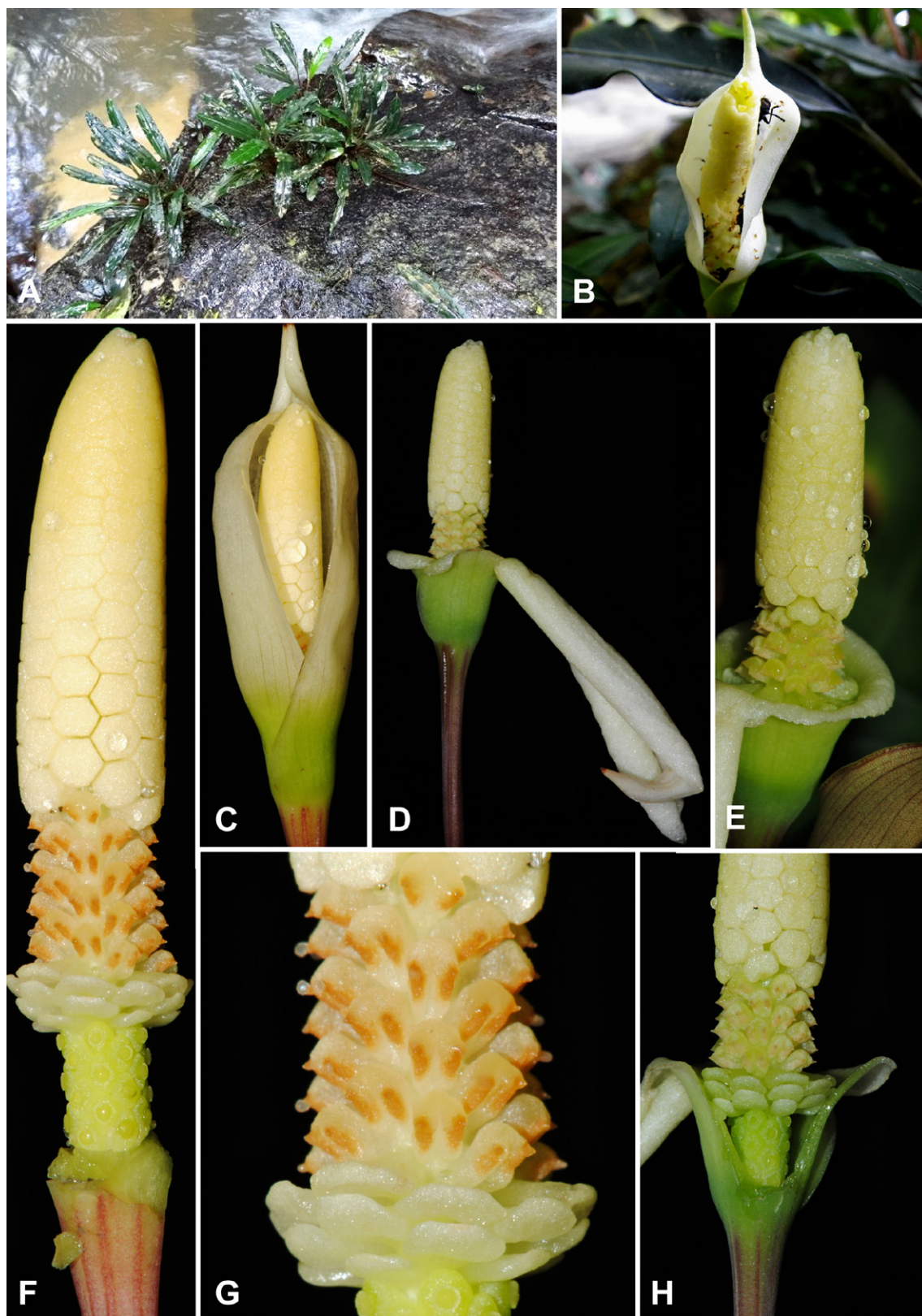


Fig. 2. *Bucephalandra aurantiitheca* – A: plants in habitat; B: inflorescence in habitat; note presence of several chrysomelid beetles, suspected pollinator; C: inflorescence at early pistillate anthesis; D: inflorescence at staminate anthesis; spathe limb is about to fall; E: inflorescence at staminate anthesis, reflexed interstice staminodes are just visible blocking entrance of persistent lower spathe; F: inflorescence at staminate anthesis; spathe artificially removed; G: detail of staminate flower zone at staminate anthesis; note pollen droplet at tips of thecae horns; H: spadix at staminate anthesis, spathe limb fallen naturally, nearside of lower spathe artificially removed; note that interstice staminodes have reflexed to seal lower spathe entrance. – Photographs: from K. Nakamoto AR-3937; A & B by K. Nakamoto; C–H by P. C. Boyce.

connective tetrahedral, with one side facing outward and upward; *thecae* inserted ventrally almost completely immersed into connective, individually very narrowly ellipsoid, c. 1 mm long \times c. 0.3 mm wide, bright orange; *thecae horns* very short, barely 0.2 mm long, nipple-like, downward-directed throughout anthesis; *appendix* \pm tapering-cylindrical, 1.5–2 cm long \times c. 5 mm in diam., cream to pale yellow; *appendix staminodes* columnar, densely arranged, trapezoidal, smooth, lowermost ones largest, c. 2 mm in diam., uppermost ones c. $\frac{1}{3}$ this size, with terminal ones irregularly polygonal, c. 0.5 mm in diam. *Fruiting spathes* and *infructescences* not seen.

Ecology — *Bucephalandra aurantiitheca* occurs on exposed granite rocks along large rivers through perhumid to moist lowland forest at between 60–90 m above sea level.

Distribution — Central W Borneo: restricted to Sekadau and Nanga Taman, Kabupaten Sekadau, Kalimantan Barat.

Etymology — Compound adjective from neo-Latin, *aurantius* (orange) and Latin, *theca* (from Greek, *thēkē*, container), referring to the staminate flower anther sacs.

Remarks — *Bucephalandra aurantiitheca* occurs at Nanga Taman with *B. chimaera*, although on different ecology (along exposed large rivers vs shady forest streams). Plants of both are similar in appearance, but readily differentiated on staminate flower characteristics (compare Fig. 23B with 23F), and in lacking pistillodes at the base of the spadix.

Commercial names — ‘Long Spath’.

Additional specimens seen (paratypes) — INDONESIA BORNEO: KALIMANTAN BARAT: Kabupaten Sekadau, Kecamatan Nanga Taman, 2 hours walk W from Simpang Tapang Perodah, c. 23 km S of Kayu Lapis and c. 19 km along main road W of Sekadau, 00°09'56.6"S, 111°03'28.7"E, 22 May 2012, K. Nakamoto AR-3940 (BO!, SAR!, SBC!) & K. Nakamoto AR-3945 (BO!, SAR!, SBC!).

3. *Bucephalandra belindae* S. Y. Wong & P. C. Boyce, **sp. nov.** – Fig. 3 & 23C.

Holotype: Indonesian Borneo, Kalimantan Barat, Kabupaten Melawi, Kecamatan Nanga Pinoh, 33 km S of Nanga Pinoh and 11 km before Kotabaru junction of logging road to Kalimantan Tengah, 00°31'46.0"S, 111°48'02.4"E, 3 Feb 2012, K. Nakamoto AR-3531 (BO!; isotypes: SAR!, SBC!, SING!).

Diagnosis — *Bucephalandra belindae* most closely resembles *B. catherinae* (NE Kalimantan) in overall ap-

pearance, but is readily distinguished by the conic spadix appendix, comprised of very few, large glassy staminodes (vs a globose spadix appendix, comprised of several small waxy staminodes). The much-elongated peduncle is shared with parapatric (but attitudinally allopatric) *B. sordidula*, from which *B. belindae* is immediately identifiable by the narrowly linear, strongly crispulate leaves, mats of trailing stems, and white (not reddish brown) thecae.

Description — Diminutive obligate rheophytic herbs c. 3 cm tall, occurring as very extensive mats of weakly-rooting interlaced stems, with much of plant hanging in water flow. *Stem* slender, c. 2 mm in diam., creeping and much-branched, with active portions sub-erect. *Leaves* forming rosettes on tips of active branches, many together; *petiole* 2–4 mm long \times c. 1 mm in diam., adaxially canaliculate, pale reddish, sheathing at extreme base, wings extended into a narrowly ligular portion to 7 mm long; *blade* very narrowly oblong-linear, 2.5–3 cm long \times c. 2 mm wide, margin very strongly undulate-crispulate, slightly to rather markedly recurved, semi-glossy dark green adaxially, reddish tinged abaxially, base cuneate, apex rounded and apiculate for c. 0.3 mm; *midrib* abaxially prominent; *primary lateral veins* 1 or 2, running almost parallel to margins and merging with leaf tip; *secondary venation* adaxially forming a \pm obscure reticulum, all other venation nearly invisible. *Inflorescence* solitary; *peduncle* greatly exceeding petioles, 4–5 cm long, longitudinally sulcate, pale green and somewhat refractive, heavily speckled pinkish red. *Spathe* broadly ovate, not constricted, c. 1 cm long; *lower spathe* funnel-form, yellowish green with pinkish speckles, persistent; *limb* inflating and gaping distally to form a narrow opening at pistillate anthesis, caducous during staminate anthesis, white with a little to considerable pinkish red speckling, dorsal median band greenish with pink speckles and staining, occasionally entire limb rose pink with darker pink speckles, tip blunt, green. *Spadix* c. 6 mm long; *pistillate zone* sessile, c. 2 mm long \times c. 2 mm in diam., with 1 (or incompletely 2) spiral(s) of pistils; *pistils* compressed globose, c. 0.5 mm in diam., bright lime-green; *stigma* sessile, rather discoid-umbonate, c. $\frac{1}{3}$ diameter of ovary, papillate at anthesis; *pistillodes* absent; *interstice* with 1 row of *scale-like staminodes*, these c. 0.7 mm long \times c. 1 mm wide, margins ventrally thickened, staminodes initially erect (pistillate anthesis), during staminate anthesis reflexing until perpendicular to spadix axis, initially pale salmon-pink, later (post-anthesis) becoming green and persisting to cover developing fruit; *staminate zone* c. 2 mm long \times c. 2.5 mm in diam., consisting of 2 (or 3) rows of flowers; *staminate flowers* pale salmon-pink; *stamen* c. 1 mm across; *filament* short; *connective* strap-like; *thecae* inserted ventrally on connective, individually ellipsoid, c. 0.4 mm long \times c. 0.2 mm wide, smooth, pale salmon-pink; *thecae horns* c. $\frac{1}{3}$ length of associated theca, ascending, stoutly setaceous; *appendix* conic-cylindric to globose, c. 2.5 mm long \times 1.5–2 mm in diam., glossy waxy white; *appen-*



Fig. 3. *Bucephalandra belindae* – A & B: plants in habitat; C & F: inflorescence at early pistillate anthesis; note slit at tip of spathe limb (F); D & E: inflorescence at staminate anthesis; most of spathe limb has been shed, with remaining portion reflexed; G: spadix at pistillate anthesis, spathe artificially removed; note that interstice staminodes are still erect, and that staminate flower thecae have yet to reflex. – Photographs: A & B from K. Nakamoto AR-3531; C, F & G from K. Nakamoto AR-3754; D & E from K. Nakamoto AR-3749; all by P. C. Boyce.

dix staminodes few, comparatively large, c. 1.5 mm in diam., rhomboidal, tops smooth. *Fruiting spathe* broadly funnel-form, c. 6 mm in diam., medium green with dense pinkish red speckles, with green shield-shaped staminodes persistent and spent distal part of spadix falling; *fruits and seeds* not seen.

Ecology — *Bucephalandra belindae* occurs solely on granite cascades with constant flowing water under perhumid lower hill to hill forest, recorded between 260–350 m above sea level.

Distribution — Known only from the type locality, where it is restricted to a single cascade a little more than 100 m long.

Eponymy — Named for Belinda Tan Cho Hiang, wife of Nakamoto Kazuya, in recognition of her long-standing support for and patience with her husband's extensive fieldwork.

Remarks — *Bucephalandra belindae* is ecologically and morphologically highly distinct, occurring as extensive mats of densely tangled long slender stems under constant water flow; it is arguable that *B. belindae* is not a true rheophyte sensu van Steenis (1981, 1987). It occurs allopatrically (same geological formation but in different ecology) with *B. sordidula*. Both species have a remarkably elongated peduncle seemingly adapting the plants to flower while otherwise underwater.

Bucephalandra belindae is most similar in overall appearance to *B. catherinae*, a conventionally rheophytic species restricted on basalt c. 450 km to the NE.

Commercial names — ‘Belinda’, ‘Fake Catherinae’.

Additional specimens seen (paratypes) — INDONESIA BORNEO: KALIMANTAN BARAT: Kabupaten Melawi, Kecamatan Nanga Pinoh, 33 km S of Nanga Pinoh and 11 km before Kotabaru junction of logging road to Kalimantan Tengah, 00°31'46"S, 111°48'02"E, 3 Feb 2012, K. Nakamoto AR-3749 (BO!) & AR-3754 (BO!, SAR!).

4. *Bucephalandra bogneri* S. Y. Wong & P. C. Boyce, **sp. nov.** – Fig. 4 & 23D.

Holotype: Malaysian Borneo, Sarawak, Bahagian Kuching, Penrissen Road, 18 miles S of Kuching, on rock along the Sungai Retien, 7 Sep 1978, J. Bogner 1366 (M!; isotypes: K!, US!).

– *Bucephalandra motleyana* sensu Bogner in Aroideana 3: 134–143, fig. 1–4. 1980, non Schott (1858).

Diagnosis — *Bucephalandra bogneri* is defined by the combination of individually distinct irregularly shaped appendix staminodes with a brain-like surface, and almost globose staminate flowers. The spadix appendix in

B. bogneri is yellow and reminiscent of that of *B. muluensis* (from Mulu National Park limestones), which latter differs by the appendix staminodes regularly rhombic to trapezoid in outline and by the brilliant green leaf blades.

Description — Small but robust obligate rheophytic herbs 6–14 cm tall, sometimes forming patches up to 50 cm across. *Stem* creeping and rooting with active portions erect, branching repeatedly, branches up to 10 cm long × c. 1.5 cm in diam. *Leaves* many together; *petiole* 6–8 cm long × c. 1.5 mm in diam., adaxially canaliculate, bright reddish purple, sheathing at extreme base, wings extended into a very narrowly triangular ligular portion to 3 cm long; *blade* elliptic to lanceolate 6–9 cm long × 2.3–3 cm wide, rather thickly coriaceous, weakly glossy dark blue-green with major veins paler adaxially, paler and reddish abaxially, base cuneate, apex rounded and apiculate for c. 4 mm, margin markedly undulate; *midrib* abaxially and adaxially prominent, strongly reddish abaxially; *primary lateral veins* c. 5 on each side, diverging at 25°–60° and running to a marginal vein; *interprimary veins* much finer; *secondary venation* adaxially ± obscure, abaxially fine. *Inflorescence* solitary, occasionally two together separated by a foliage leaf; *peduncle* exceeding petioles, 4–5 cm long, conspicuously longitudinally sulcate and occasionally distally winged, reddish purple, this colour derived from dense tiny speckles. *Spathe* broadly ovate, not constricted, 2.5–3 cm long; *lower spathe* funnel-form, lime-green, insertion on peduncle reddish purple, persistent; *limb* inflating and gaping distally to form a narrow opening at pistillate anthesis, caducous during staminate anthesis, glistening white, apiculate for c. 3 mm, apiculum green. *Spadix* c. 1.5 cm long, very shortly stipitate; *stipe* less than 0.3 mm long, light green; *pistillate zone* c. 3 mm long × c. 3 mm in diam., with c. 3 spirals of pistils; *pistils* slightly densely arranged, cylindric-globose, c. 2 mm long × c. 0.5 mm in diam., bright lime-green; *stigma* sessile, rather discoid-umbonate, c. ½ diameter of ovary, papillate at anthesis; *pistillodes* in a single incomplete row at base of pistillate zone, squat fusiform with a short terminal beak, in all c. 0.2 mm in diam., glossy white; *interstice* with 2 rows of *scale-like staminodes*, these c. 2 mm long × c. 1 mm wide, ventrally slightly umbonate, staminodes initially erect (pistillate anthesis), during staminate anthesis reflexing until almost downturned with staminode beyond mid-part ascending, initially white with narrowed base green, later (post-anthesis) becoming green and persisting to cover developing fruit; *staminate zone* 4–6 mm long × 4–5 mm in diam., consisting of 4 or 5 rows of flowers; *staminate flowers* creamy yellow; *stamen* comparatively large, c. 1.5 mm across; *filament* short but clearly defined; *connective* cap-like and dorsally arched, pale yellow; *thecae* inserted ventrally on connective, with appearance of being suspended from it, paler than connective, individually ellipsoid,

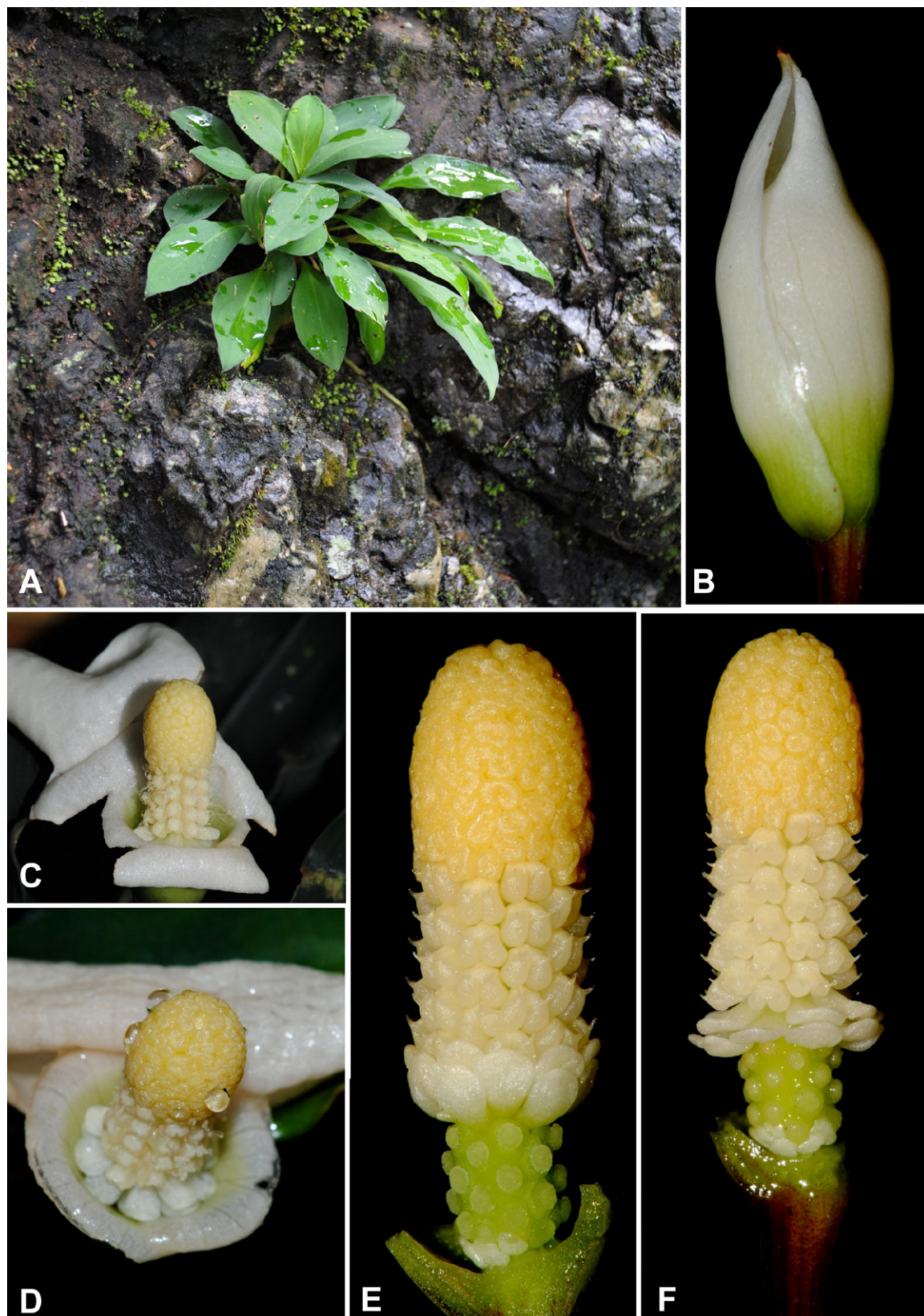


Fig. 4. *Bucephalandra bogneri* – A: plant in habitat on basalt; B: inflorescence at pistillate anthesis; note slit toward tip of spathe limb; C & D: inflorescence at staminate anthesis; spathe limb is being shed; note (C) reflexed staminate flowers and thecae horns with a pollen droplet at tip; note, too, (D) that interstice staminodes have reflexed to block entrance of lower spathe; E: spadix at pistillate anthesis, spathe artificially removed; interstice staminodes are still erect and staminate flower thecae have yet to reflex; F: spadix at staminate anthesis, spathe artificially removed; note that interstice staminodes and staminate flower thecae have reflexed. – Photographs: A from P. C. Boyce & S. Y. Wong AR-2435; B–F from P. C. Boyce & al. AR-94; all by P. C. Boyce.

c. 1 mm long \times c. 0.4 mm wide, smooth; *thecae horns* c. $\frac{1}{4}$ length of associated theca, ascending, stiffly setaceous; *appendix* bullet-shaped to globose, 4–5 mm long \times 3–4 mm in diam., bright yellow; *appendix staminodes* mostly squat cylindrical, 0.5–1 mm in diam., tops brain-like, densely arranged, lowermost ones transitioning to staminate flowers in appearance. *Fruiting spathe* broadly funnel-form, c. 1 cm in diam., medium green, with green shield-shaped staminodes persistent and spent distal part of spadix falling; *berry* depressed globose, 1–1.8 mm long \times 1–1.5 mm in diam., medium green, with numerous seeds, berries forming a hemispherical cluster protected by persistent staminodes, later pushed off and falling to reveal mature fruits; *fruits* decomposing at maturity, forming a pulp with seeds held in persistent lower spathe; *seed* not seen.

Ecology — *Bucephalandra bogneri* is restricted to alkaline geologies, on limestone (e.g. at Pichin, Padawan), or on basalt (e.g. at Ranchan, Saroban), under perhumid to moist lowland to lower hill forest between 30–350 m above sea level.

Distribution — Penrissen and Serian area, Bahagian Kuching, Sarawak.

Eponymy — Named for Dr Josef Bogner (Munich Botanic Garden), who has contributed so much to the knowledge of aroids.

Remarks — *Bucephalandra bogneri* has an obligate affinity with alkaline substrates, shared with *Piptospatha viridistigma* P. C. Boyce & al., with which *B. bogneri* frequently co-occurs, as at Ranchan. Their ecology, however, differs somewhat. *P. viridistigma* favours shaded flat expanses of stony riverside, with its roots frequently inundated, whereas *B. bogneri* is restricted to the leeward side of large boulders, in which position it is often subjected to periods of dryness.

Non-flowering plants of *Bucephalandra bogneri* are very reminiscent of those of *B. akantha*, although the species are readily distinguished on spadix characteristics and ecology.

Bucephalandra bogneri was figured by Bogner (1980) as *B. motleyana* when clarifying the interpretational issues of *Bucephalandra* arising from mistakes in Schott's original publication (see also Boyce & Wong 2012).

Commercial names — None.

Additional specimens seen (paratypes) — MALAYSIAN BORNEO: SARAWAK: Bahagian Kuching: Padawan, Kampung Belimbing, 01°06'N, 110°38'E, 28 Nov 2003, P. C. Boyce & Jeland ak Kisai AR-94 (SAR!). Bahagian Samarahan: Serian, along the Sungai Ranchan, 20 Sep 1978, J. Bogner 1447 (K!, M!, US!); Serian, Taman Rekreasi Ranchan, 01°08'34.9"N, 110°35'02.4"E, 11 Apr 2009,

P. C. Boyce & Wong Sin Yeng AR-2435 (SAR!); Serian, Pichin, Gunung Kedadum, Sugun Kerang, 1 Aug 2010, P. C. Boyce & al. AR-3038 (SAR!); Serian, Kampung Saroban, Saroban Waterfalls, 01°08'41.3"N, 110°35'40.4"E, 22 Oct 2012, R. Tseu AR-4067 (SAR!).

5. *Bucephalandra catherineae* P. C. Boyce, Bogner & Mayo in Bot. Mag. 12: 152. 1995. – Fig. 23E.

Holotype: Indonesian Borneo, Kalimantan Utara, Kabupaten Malinau, Kecamatan Kayan Hulu, Apo Kayan, E of Long Nawan, Gunung Sungai Pendau, E ridge, c. 01°56'N, 115°01'E, 14 Oct 1991, E. F. de Vogel & P. J. Cribb 9210 (L!; isotype: K – spirit coll. no 57575!).

Description — See Boyce & al. (1995).

Ecology — *Bucephalandra catherineae* is known exclusively from basalt riverside boulders under wet upper hill forest at c. 600 m above sea level.

Distribution — Known with certainty only from the type locality, but see under Remarks.

Eponymy — Dedicated to the botanical artist Eleanor Catherine in recognition of the painstaking illustration work she undertook for The genera of Araceae project (Mayo & al. 1997).

Remarks — Morphologically very similar plants are known from shaded riverside granites at Nanga Pinoh (Kabupaten Melawi, Kalimantan Barat), some 450 km to the SW of *Bucephalandra catherineae*. These have yet to flower in cultivation and confirmation of their identity is not yet secure.

Commercial names — None.

6. *Bucephalandra chimaera* S. Y. Wong & P. C. Boyce, **sp. nov.** – Fig. 5 & 23F.

Holotype: Indonesian Borneo, Kalimantan Barat, Kabupaten Sekadau, Kecamatan Nanga Taman, environs of Nanga Taman, 4 Apr 2012, K. Nakamoto AR-3846 (BO!; isotypes: SAR!, SBC!, SING!).

Diagnosis — *Bucephalandra chimaera* most closely resembles *B. aurantiitheca* but may be distinguished by the spreading (not upward-arching) staminate flowers, and by the ascending thecae horns.

Description — Small obligate rheophytic herbs c. 17 cm tall. *Stem* erect, later decumbent and rooting with active portion sub-erect, c. 1.5 cm in diam. *Leaves* many together, erect-arching; *petiole* 6–9 cm long \times c. 2 mm in diam., conspicuously longitudinally sulcate, brownish green, sheathing at extreme base, wings extend-

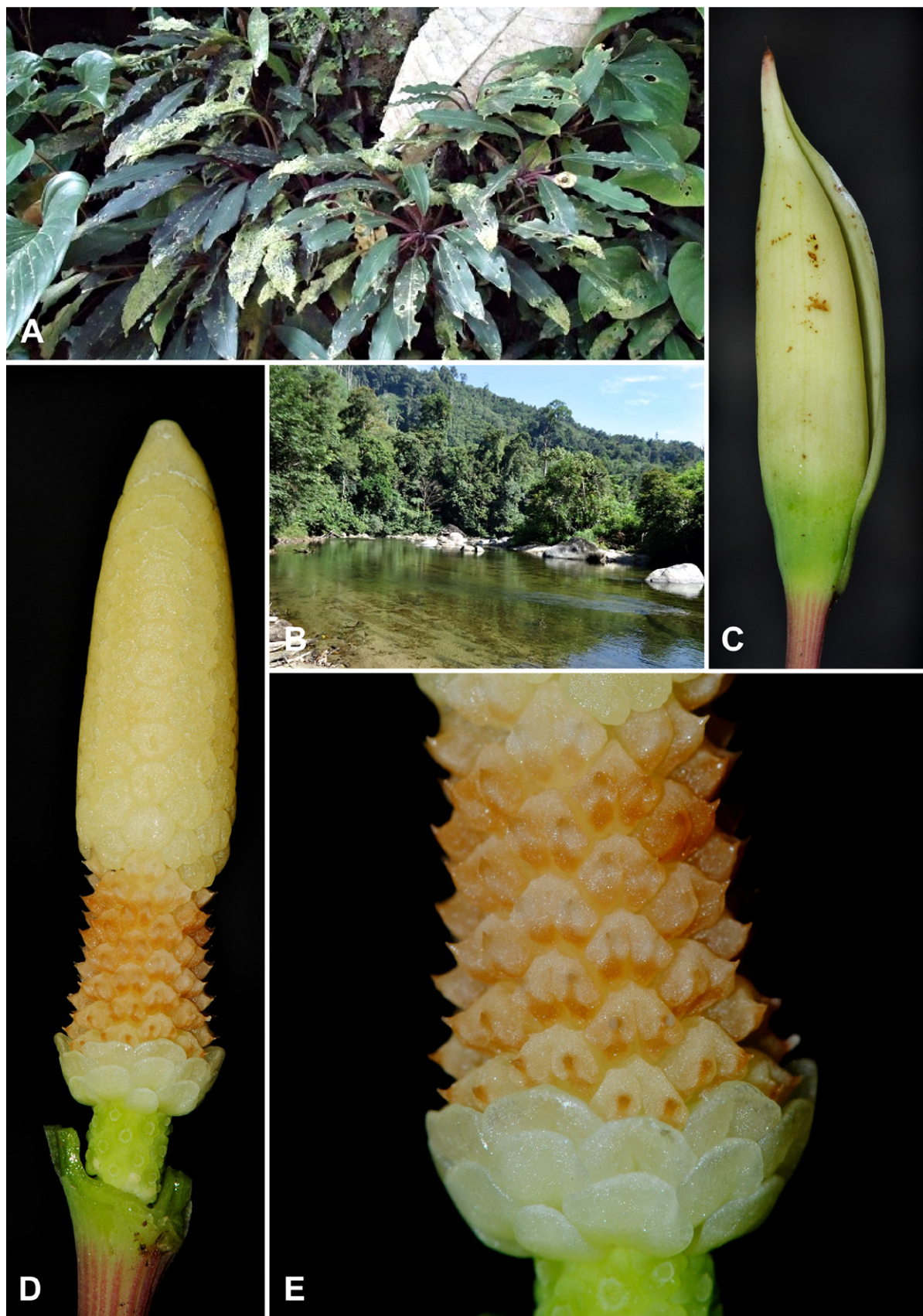


Fig. 5. *Bucephalandra chimaera* – A: plants in habitat; B: habitat; *B. chimaera* occurs at bases of large granite boulders along river bank; C: inflorescence at pistillate anthesis; D: spadix at pistillate anthesis, spathe artificially removed; note that interstice staminodes are still erect and that staminate flower thecae have yet to reflex; E: detail of staminate flower zone at pistillate anthesis. – Photographs: from K. Nakamoto AR-3846; A & B by K. Nakamoto; C–E by P. C. Boyce.

ed into a narrowly triangular ligular portion c. 4 cm long; *blade* oblong-elliptic to elliptic, 9–12 cm long × 2–3 cm wide, coriaceous, semi-glossy emerald-green adaxially, yellowish green abaxially, base cuneate, apex acute and apiculate for c. 5 mm, margin weakly undulate; *midrib* abaxially prominent, dull red, adaxially slightly raised; *primary lateral veins* c. 6 on each side diverging at c. 30° and running to a rather conspicuous marginal vein; *interprimary veins* alternating with primaries, weaker than primaries, reddish; *secondary venation* adaxially obscure, abaxially forming a faint reticulate pattern; *tertiary venation* obscure. *Inflorescence* solitary; *peduncle* exceeding petioles, 5–11 cm long × c. 2.5 mm in diam. (average), longitudinally sulcate, pale green suffused reddish brown with ridges darker red. *Spathe* oblong-ovate, not constricted, 4–4.5 cm long; *lower spathe* initially narrowly funnel-form, later (staminate anthesis) flaring, medium semi-glossy green, persistent; *limb* slightly inflating and gaping distally at pistillate anthesis, opening widely almost to persistent lower spathe during staminate anthesis, caducous during late or post-staminate anthesis, with margins recurving, and limb often retaining a slender connection to lower spathe, greenish ivory, acuminate for c. 6 mm and apiculate for c. 1.5 mm, apiculum medium green. *Spadix* c. 3.5 cm long; *pistillate zone* c. ½ width of remainder of spadix, sessile, 3.5–5 mm long × c. 3 mm in diam., with c. 3 rows of pistils; *pistils* very closely appressed, rhombic-cylindric, c. 0.5 mm in diam., pale green; *stigma* sessile, button-like, c. ½ diameter of ovary, papillate at anthesis; *pistillodes* few, interspersed between lowermost spiral of pistils at their junction with spathe, spatulate, c. 0.5 mm long, glossy white; *interstice* with c. 3 rows of *scale-like staminodes*, these c. 2 mm long × 1.8 mm wide, margin thickened, staminodes initially erect (pistillate anthesis), reflexing during staminate anthesis until sub-perpendicular with spadix axis, initially greenish white, later (post-anthesis) becoming green and persisting to cover developing fruit; *staminate zone* c. 1 cm long × c. 6 mm in diam., consisting of c. 7 rows of flowers; *staminate flowers* pale orange; *stamen* large, c. 1 mm tall × c. 2 mm wide, overall pale orange; *filament* short, conspicuous; *connective* tetrahedral, with one side facing outward and upward; *thecae* inserted ventrally into connective, and almost completely immersed in connective tissues, individually very narrowly ellipsoid, c. 1 mm long × c. 0.3 mm wide, bright orange; *thecae horns* very short, barely 0.2 mm long, nipple-like, upward directed during pistillate anthesis, later (by reflexing of stamen filament during staminate anthesis), downward-directed; *appendix* ± tapering cylindrical, 1.5–2 cm long × 6–8 mm in diam.; *appendix staminodes* trapezoidal-cylindric, densely arranged, truncate, smooth, lowermost ones largest, c. 2 mm in diam., uppermost ones c. ½ this size, with terminal ones irregular and c. 0.5 mm in diam. *Fruiting spathes* and *infructescences* not seen.

Ecology — *Bucephalandra chimaera* occurs on granite boulders along small streams under perhumid lowland forest at c. 90 m above sea level.

Distribution — Known only from the type locality, where it co-occurs, although in a different ecological niche, with *B. aurantiithec*a (see Remarks under *B. aurantiithec*a).

Etymology — From the Chimaera of Greek mythology, the offspring of Typhoeus and Echidna, comprised of parts from a lion, a goat, and a snake. The name is chosen in allusion to this new species resembling one species by its leaves, another by its inflorescences, and a third by its staminate flowers.

Remarks — The occurrence of two *Bucephalandra* species at the same locality is highly unusual. *Bucephalandra chimaera* is vegetatively very similar in appearance to *B. aurantiithec*a (see above), with which it co-occurs although in a discrete ecology, but shows marked and stable differences in spadix morphology (compare Fig. 23F with 23B).

Commercial names — ‘Chimera’.

7. *Bucephalandra chrysokoupa* S. Y. Wong & P. C. Boyce, **sp. nov.** – Fig. 6 & 23G.

Holotype: Indonesian Borneo, Kalimantan Utara, Kabupaten Nunukan, Kecamatan Mentarang Hulu, Long Berang, 03°48'25.2"N, 116°11'24.7"E, 18 Jun 2012, K. Nakamoto AR-3977 (BO!; isotypes: SAR!, SBC!, SING!).

Diagnosis — *Bucephalandra chrysokoupa* is uniquely distinguished from all other *Bucephalandra* species by the combination of the golden yellow to medium bright orange spathe limb, and by the interstice staminodes having minutely serrate tips.

Description — Small tufted obligate rheophytic herbs c. 10 cm tall, occurring as individual plants. *Stem* erect, all but older portions obscured by sheathing leaf bases. *Leaves* to c. 15 together; *petiole* 3–4.5 cm long × c. 2 mm in diam., adaxially canaliculate, dull brownish green, sheathing at extreme base, wings extended into a very narrowly triangular ligular portion to 2.5 cm long; *blade* narrowly elliptic, 6–7 cm long × 2–2.5 cm wide, rather thinly coriaceous, glossy bright medium green adaxially, paler and matte abaxially and occasionally tinged brownish red, base cuneate, apex acute and apiculate for c. 1.5 mm, margin smooth to somewhat undulate; *midrib* abaxially and adaxially somewhat prominent, reddish abaxially; *primary lateral veins* c. 3 on each side, diverging at 25°–60° and running to a marginal vein; *interprimary veins* alternating with primaries, very much less conspicuous; *secondary venation* adaxially ± obscure;

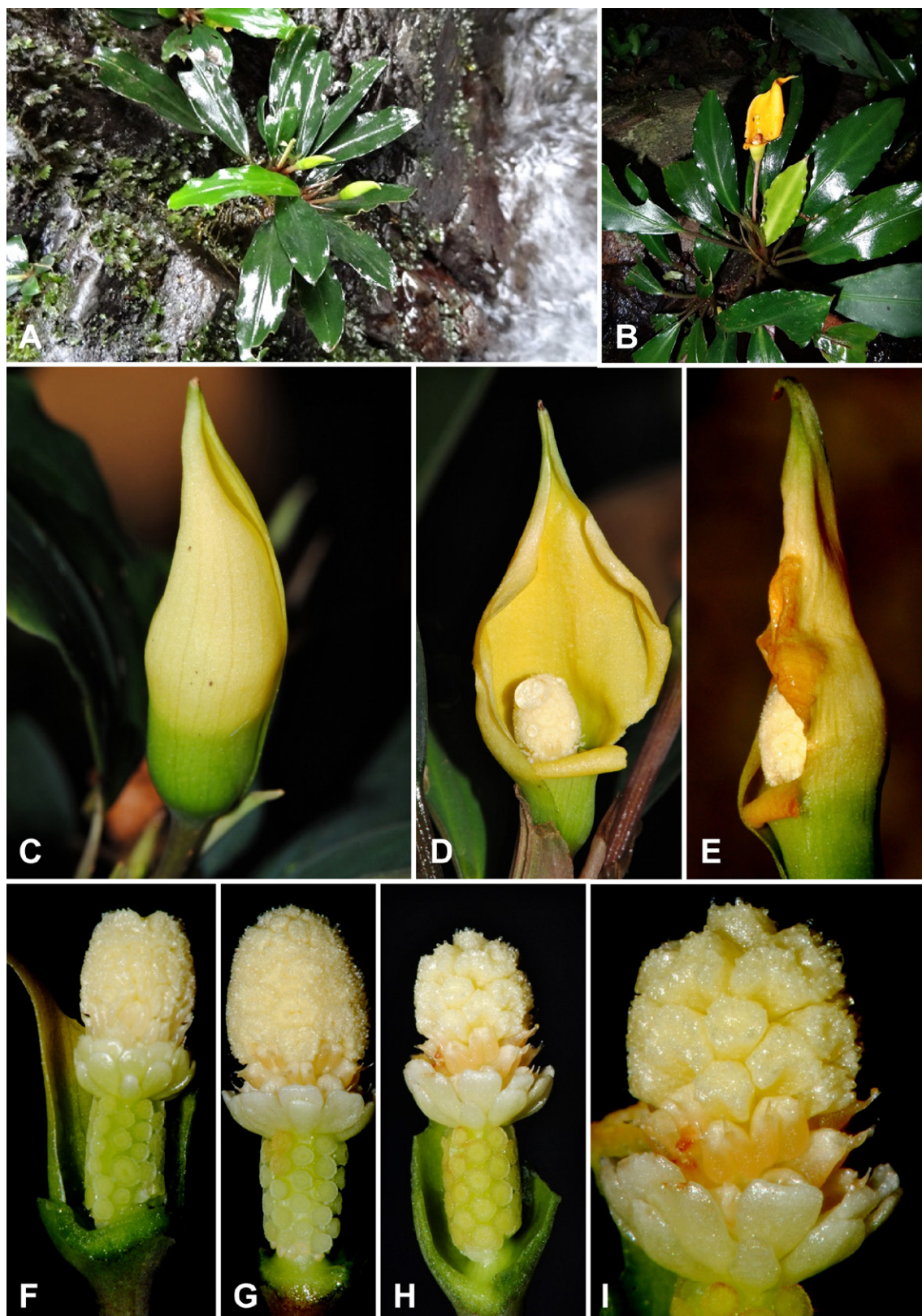


Fig. 6. *Bucephalandra chrysokoupa* – A & B: plants in habitat; C: inflorescence at early pistillate anthesis; note slit at tip of spathe limb; D: inflorescence at onset of staminate anthesis; E: inflorescence at peak of staminate anthesis; note that spathe limb is starting to decay and separate from lower persistent part; F: spadix at pistillate anthesis, spathe limb and nearside part of lower spathe artificially removed; note that interstice staminodes are still erect and that staminate flower thecae have yet to reflex; G: spadix at onset of staminate anthesis, spathe artificially removed; note that interstice staminodes are beginning to lower; H & I: spadix at staminate anthesis. Variation in appendix staminodes is clearly seen in F–I. – Photographs: from K. Nakamoto AR-3977; A & B by K. Nakamoto; C–I by P. C. Boyce.

tertiary venation abaxially forming a faint tessellate reticulum. *Inflorescence* solitary; *peduncle* exceeding petioles, 3–6 cm long, smooth to very slightly longitudinally sulcate, greenish red. *Spathe* broadly turbinate to oblong-conic, not constricted, up to 3.5 cm long; *lower spathe* funnel-form, dull green, persistent; *limb* inflating, with a distal slit appearing at pistillate anthesis, then semi-deliquescent-caducous, golden yellow to medium orange, somewhat waxy, rostrate for c. 1 cm and then apiculate for c. 3 mm. *Spadix* 1.1–1.3 cm long, very shortly stipitate; *stipe* c. 0.2 mm long, pale green; *pistillate zone* 3–4.2 mm long × c. 1.5 mm in diam., with 4 or 5 spirals of pistils; *pistils* cylindric, c. 0.5 mm in diam., medium green; *stigma* sessile, discoid, sub-equalling diameter of ovary, papillate at anthesis; *pistillodes* absent; *interstice* with c. 2 rows of *scale-like staminodes*, these c. 3 mm long × 1.8 mm wide, tips shallowly retuse, serrate, staminodes initially (pistillate anthesis) erect, then reflexing during staminate anthesis, initially white, later (post-anthesis) becoming green and persisting to cover developing fruit; *staminate zone* 2–3 mm long × c. 3.5 mm in diam., consisting of c. 2 rows of flowers; *staminate flowers* creamy white; *stamen* c. 1.2 mm across × c. 2 mm long; *filament* very short, initially erect (pistillate anthesis), reflexing during staminate anthesis; *connective* strap-shaped; *thecae* inserted ventrally on connective, narrowly ellipsoid, c. 1 mm long × c. 0.3 mm wide, smooth; *thecae horns* c. ½ length of associated theca, setaceous, upward-pointing during pistillate anthesis, later spreading; *appendix* globose to bullet-shaped, 4–5 mm long × 3–4 mm in diam., creamy white to pale yellow; *appendix staminodes* obpyramidal, c. 1 mm in diam., tops echinate, occasionally coarsely so. *Fruiting spathe* narrowly funnel-form, c. 1 cm in diam., medium glossy green, with shield-shaped staminodes persistent, turning green, spent distal part of spadix falling; *fruits* and *seeds* not seen.

Ecology — *Bucephalandra chrysokoupa* occurs on granite riverside boulders under lowland moist forest at c. 170 m above sea level.

Distribution — Known only from the type locality and the immediately surrounding area.

Etymology — From Greek adjective, *chrysos* (golden) and Greek noun, *koupa* (cup), in reference to the diagnostic golden to orange spathe.

Remarks — *Bucephalandra chrysokoupa* is a remarkable and also highly attractive species, unique by the combination of the golden to orange spathe limb and the interstice staminodes with serrate tips. The appendix staminodes are also serrate to a variable degree: in extreme clones the appendix resembles a coarse stippling paintbrush.

Commercial names — ‘Marie’, ‘Miranda’, ‘Juliet’.

8. *Bucephalandra diabolica* S. Y. Wong & P. C. Boyce, **sp. nov.** – Fig. 7 & 23H.

Holotype: Indonesian Borneo, Kalimantan Barat, Kabupaten Melawi, Kecamatan Sayan, Bukit Baka-Bukit Raya National Park, Bukit Baka, 00°24'45.2"S, 111°59'43.9"E, 1 Sep 2012, *M. Lo* AR-4027 (BO!; isotypes: SAR!, SBC!, SING).

Diagnosis — *Bucephalandra diabolica* is most similar to *B. pygmaea* and *B. sordidula*, but differs from both by the thecae horns at least as long as the rest of the staminate flower. *Bucephalandra diabolica* also differs from *B. sordidula* by the white (not reddish brown) thecae.

Description — Diminutive obligate rheophytic herbs c. 2 cm tall, occurring in extensive patches. *Stem* creeping with active portion sub-erect, branching repeatedly, c. 1–2.5 mm in diam. *Leaves* appressed to ground, scattered along stems and forming small clusters at shoot tips; *petiole* 0.5–1 cm long × c. 2 mm in diam., adaxially canaliculate, greenish brown, sheathing at extreme base, wings extended into a very narrowly triangular ligular portion to 1 cm long; *blade* obovate, 3–5 cm long × 1–1.5 cm wide, thinly coriaceous, metallic bluish olive-green adaxially, paler and reddish abaxially, base cuneate to sub-decurrent, apex rounded and apiculate for c. 1 mm, margin usually weakly undulate; *midrib* adaxially somewhat prominent, abaxially much finer, although reddish and therefore conspicuous; *primary lateral* and *interprimary veins* very fine and not differentiated, c. 10 veins per side; *secondary venation* abaxially very fine and forming faint reticulum. *Inflorescence* solitary; *peduncle* slender, exceeding petioles, c. 3 cm long × c. 1.5 mm in diam., conspicuously longitudinally sulcate and distally winged, pale brownish with reddish ridges. *Spathe* broadly ovate, not constricted, c. 1.5 cm long; *lower spathe* widely funnel-form, very pale pinkish green, persistent; *limb* inflating, then gaping, then caducous, white, apiculate for c. 2 mm. *Spadix* 5–8 mm long; *pistillate zone* c. 1 mm long × c. 3 mm in diam., with 1 spiral of pistils; *pistils* compressed globose, c. 0.5 mm in diam., yellow-green; *stigma* sessile, umbonate, c. ½ diameter of ovary, papillate and with a conspicuous stigmatic droplet at anthesis; *pistillodes* absent; *interstice* with c. 2 rows of *scale-like staminodes*, these c. 1.5 mm long × c. 0.8 mm wide, very shallowly concave, very pale pink with darker pink minute speckles; *staminate zone* 2–3 mm long × c. 2.5 mm in diam., consisting of c. 3 irregular rows of flowers; *staminate flowers* brownish pink; *stamen* large, c. 1 mm across, brownish pink; *filament* very short; *connective* triangular-prismatic; *thecae* inserted ventrally, ellipsoid, c. 1 mm long × c. 0.3 mm wide, smooth; *thecae horns* longer than remainder of stamen, setaceous, upward curving; *appendix* globose to bluntly cylindrical, 1–2 mm long × 1.5–2 mm in diam., pinkish cream; *appendix staminodes* very few, fused, truncate, 0.5–1 mm in diam., upper surface smooth and glossy. *Fruiting*



Fig. 7. *Bucephalandra diabolica* – A–C: plants in habitat; C: inflorescence at staminate anthesis; note spathe limb is lost; D & E: inflorescence at pistillate anthesis; note slit at tip of spathe limb; F: spadix just before staminate anthesis, spathe artificially removed; note that staminodes are beginning to lower. – Photographs: from *M. Lo AR-4027*; A–C by M. Lo; D–F by P. C. Boyce.

spathe widely and shallowly funnel-form, c. 1 cm in diam.; *fruits* and *seeds* not seen.

Ecology — *Bucephalandra diabolica* occurs on granite riverside rocks and steep rocky riverbanks under moist lowland forest at approximately 50 m above sea level.

Distribution — Known only from Bukit Baka, the type locality.

Etymology — From Greek, *diabolos* (the Devil), in fanciful allusion to the form of the staminate flower, with triangular staminate flowers and erect thecae resembling the head and horns of the Devil.

Remarks — *Bucephalandra diabolica* belongs to the very probably highly speciose *Bucephalandra* Pygmaea Complex, which aside from *B. pygmaea* (Becc.) P. C. Boyce & S. Y. Wong includes *B. sordidula*, described in this paper, and very probably numerous other taxonomic novelties.

Commercial names — None.

9. *Bucephalandra elliptica* (Engl.) S. Y. Wong & P. C. Boyce, **comb. nov.** \equiv *Microcasia elliptica* Engl. in Bull. Reale Soc. Tosc. Ort. 4: 299. 1879. – Fig. 8 & 231. Holotype: Malaysian Borneo, Sarawak, Nov 1866, *O. Beccari* PB 2817 (FI-B!).

Description — Small solitary obligate rheophytic herbs to 20 cm tall. *Stem* creeping and rooting with active portion sub-erect, c. 1.3 cm in diam. *Leaves* c. 6 together; *petiole* 5–6 cm long \times c. 2 mm in diam., adaxially canalliculate, medium green, sheathing at extreme base, wings extended into a very narrowly triangular ligular portion to 3 cm long; *blade* lanceolate, rather oblique, 9–13 cm long \times 3–4 cm wide, somewhat coriaceous, semi-glossy medium green adaxially, paler green abaxially with darker green veins, base rounded, apex acuminate, apiculate for c. 2.5 mm, margin undulate, quite strongly so in larger individuals; *midrib* abaxially and adaxially prominent; *primary lateral* and *interprimary veins* not differentiated, together amounting to c. 8 per side, diverging at c. 30° and running to a marginal vein; *secondary venation* adaxially \pm obscure, abaxially fine; *tertiary venation* adaxially obscure, abaxially forming a faint tessellate reticulum. *Inflorescence* solitary; *peduncle* fairly stout, exceeding petioles, 6–10 cm long \times c. 2 mm in diam., terete, dull medium green. *Spathe* oblong-ovate, not constricted, c. 6 cm long; *lower spathe* narrowly funnel-form, bright green, shading to yellow, persistent; *limb* inflating, producing a slit near tip, then crumpling-caducous, glossy white, rostrate for c. 1.5 cm, and apiculate for c. 2 mm, apiculum green. *Spadix* 2–3 cm long; *pistillate zone* c. 7–9 mm long \times 3–4 mm wide, with c. 3 spirals of pistils; *pistils* dense, rhomboidal-cylindric, c. 0.5 mm in diam., lime-

green; *stigma* sessile, umbonate, c. ½ diameter of ovary, impressed with edges of pistil forming a raised rim, papillate and with a conspicuous stigmatic droplet at anthesis; *pistillodes* lorate-clavate, c. 1.5 mm long, glossy white; *interstice* with 2 rows of *scale-like staminodes*, these c. 2 mm long \times c. 2 mm wide, ventrally with median-line swollen and distally somewhat spatulate, pale creamy white with claw green; *staminate zone* 1–1.5 cm long \times 1–1.5 cm in diam., consisting of 5–7 rows of flowers; *staminate flowers* upward-directed during pistillate anthesis, reflexing to almost perpendicular with spadix axis during staminate anthesis, creamy white; *stamen* large, c. 2 mm across \times c. 1.5 mm tall; *filament* short; *connective* triangular-prismatic; *thecae* inserted ventrally, gibbose-ellipsoid, c. 1 mm long \times c. 0.5 mm wide, smooth; *thecae horns* c. ¼ length of associated theca, setaceous, upward-curved; *appendix* bluntly cylindrical to fusiform, 2–3 cm \times 1–1.7 cm in diam., cream; *appendix staminodes* irregularly rhombic-cylindric, lowermost in groups of 3, truncate, 0.5–1 mm in diam., top surface papillate. *Fruiting spathe* widely and shallowly funnel-form, c. 1 cm in diam. \times c. 1.5 cm tall; *fruits* and *seeds* not seen.

Ecology — *Bucephalandra elliptica* occurs on sandstone riversides and stream boulders under open lowland perhumid forest at c. 150 m above sea level.

Distribution — SW Sarawak. Known with certainty only from Sri Aman. See Remarks for other potential locations.

Remarks — *Bucephalandra elliptica* is highly distinctive, with the non-flowering adult plants resembling a juvenile *Ooia* S. Y. Wong & P. C. Boyce. *Bucephalandra elliptica* is one of a group of species with well-defined rhomboidal appendix staminodes. Among these it is unique by the appendix accounting for only about half the spadix.

Beccari's type collection makes no mention of the collecting locality, although it is dated as collected in November 1866. From this date it is possible to speculate on a probable area for the type locality. Beccari's itinerary for November 1866 is entirely in SW Sarawak: "middle of November [1866] starting to the upper waters of the Sarawak River, Tappo Kakas [01°11'30"N, 110°12'30"E], G[unung] Wa [modern name not known with certainty, perhaps Gunung Seraong] (19 Nov), Pan[g]kalan Ampat [01°11'00"N, 110°15'00"E], Senna [Senah Sebuang, 01°06'15"N, 110°16'30"E] (23 Nov), G[unung] Braam [Braang, 01°13'30"N, 110°16'00"E], Koom [not located] (26 Nov)" see <http://www.nationaalherbarium.nl/FMCollectors/B/BeccariO.htm#1866>.

Additional specimens seen — MALAYSIAN BORNEO: SARAWAK: Bahagian Sri Aman: Simunjan, Pantu, Jaong, near Pantu, 01°10'58.8"N, 110°54'00.0"E, 23 May 2011, K. Nakamoto AR-3563 (SAR) & AR-3564 (SAR).

Commercial names — None.

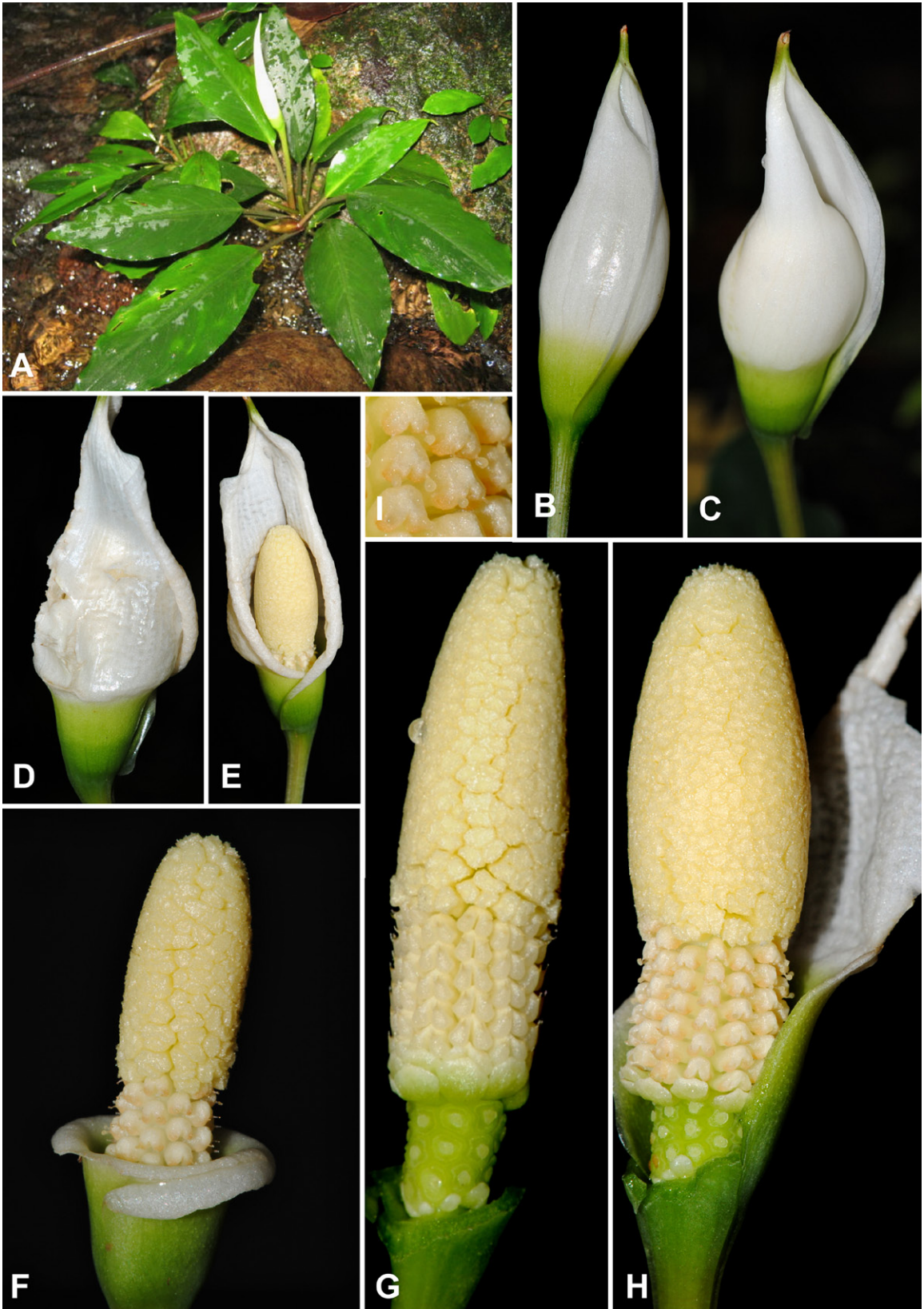


Fig. 8. *Bucephalandra elliptica* – A: plant in habitat; B & C: inflorescence at early (B) and mid- (C) pistillate anthesis; note changes in spathe limb shape; D & E inflorescence at staminate anthesis, with spathe limb beginning to deliquesce; F: inflorescence at peak of staminate anthesis; note that spathe limb is mostly now separated from lower persistent part; G: spadix at pistillate anthesis, spathe limb artificially removed; note that interstice staminodes are still erect and that staminate flower thecae have yet to reflex; H: spadix at onset of staminate anthesis, spathe partially artificially removed; note that interstice staminodes have lowered and that thecae of staminate flowers have reflexed. – Photographs: from K. Nakamoto AR-3564; A by M. Lo; B–H by P. C. Boyce.

10. *Bucephalandra forcipula* S. Y. Wong & P. C. Boyce, **sp. nov.** – Fig. 9 & 23J.

Holotype: Indonesian Borneo, Kalimantan Barat, Kabupaten Sekadau, Kecamatan Nanga Taman, SE of Nanga Taman, Gunung Tajam, E slope, 00°27'35.4"S, 111°02'03.2"E, 5 Feb 2012, K. Nakamoto AR-3772 (BO!; isotypes: SAR!, SBC!, SING!).

Diagnosis — *Bucephalandra forcipula* is distinctive among known species by the combination of clawed hastate staminate flowers, with the entire stamen (as opposed to the thecae+connective) flexing downward from the base at staminate anthesis, and the connective with a flat dorsal surface, with verrucate margins, the thecae separated by a deep sinus, and the thecae horns stout, spreading, and deep orange-brown. The large (up to 17 × 8 cm) elliptic blue-green leathery leaf blades are also uniquely diagnostic.

Description — Medium sized, robust facultative rheophytic herbs up to 30 cm tall. *Stem* initially erect, later much-elongating and becoming decumbent and rooting from behind active tip, with active portion erect, oldest stems up to 25 cm long × 2 cm in diam., although usually less, greenish brown. *Leaves* to c. 10 together; *petiole* 8–10 cm long × c. 3 mm in diam., scabridulous, adaxially narrowly canaliculate, dull pinkish brown to medium matte red, sheathing at extreme base, wings extended into a very narrowly triangular ligular portion to 5 cm long; *blade* elliptic, 10–14 cm long × 5–6 cm wide, rather thickly softly coriaceous, weakly glossy bluish grey to deep green, paler abaxially, base obtuse to rounded-cuneate, apex rounded and apiculate for c. 3 mm, margin usually straight; *midrib* abaxially and adaxially prominent; *primary lateral* and *interprimary veins* not differentiated, c. 8 on each side, diverging at 25°–60° and running to an orange marginal vein; *all other venation* obscure. *Inflorescence* solitary, occasionally paired with a conspicuous prophyll between; *peduncle* exceeding petioles, 8–12 cm long × c. 3 mm in diam., weakly longitudinally angular, pale reddish brown. *Spathe* narrowly ovate, not constricted, 8–10 cm long; *lower spathe* funnel-form, green, persistent; *limb* gaping distally at pistillate anthesis, caducous during staminate anthesis, white, rostrate for c. 1.5 cm, apiculate for c. 5 mm, apiculum green. *Spadix* 4–4.5 cm long; *pistillate zone* somewhat obliquely inserted on spathe, 4–7 mm long × c. 7 mm in diam., with 3 or 4 spirals of pistils; *pistils* cylindric-globose in plan view, c. 1.5 mm in diam., green; *stigma* sessile, discoid with a deep, narrow central pit, slightly wider than ovary, sticky papillate at anthesis; *pistillodes* 1–3 at base of pistillate zone, squat fusiform, c. 0.5 mm in diam., white; *interstice* with 3 or 4 rows of *scale-like staminodes*, these c. 2 mm long × c. 2 mm wide, each somewhat reduplicate with tip spathulate, initially white, later (post-anthesis) becoming green and persisting to cover developing fruit; *stami-*

nate zone 1.5–1.8 cm long × c. 1 cm in diam., consisting of 7–9 rows of flowers; *staminate flowers* creamy white; *stamen* c. 2 mm across; *filament* long, reflexing during staminate anthesis to reveal tops of Y-shaped connective; *connective* cuneate (Y-shaped in plan view); *thecae* inserted distally and ventrally, with a deep suture between, individually rhombic, c. 1 mm long × c. 0.5 mm wide, smooth, cream; *thecae horns* equalling associated theca, stiffly setaceous, downward and laterally spreading, initially pale cream, becoming deep orange during staminate anthesis; *appendix* bullet-shaped, 1.5–2 cm long × c. 1 cm in diam. (at widest part), cream; *appendix staminodes* rhomboidal-obpyramidal, lowermost ones truncate with a central depression, c. 1 mm in diam., upper surface papillate. *Fruiting spathe* funnel-form, c. 2 cm in diam., with shield-shaped staminodes persistent, turning green, spent distal part of spadix falling; *fruits* and *seeds* not seen.

Ecology — *Bucephalandra forcipula* is rheophytic along the edges of exposed granite waterfalls under moist hill forest at approximately 350 m above sea level.

Distribution — Known only from Gunung Tajam, on the extreme NW flanks of the Schwaner Mountains, Kalimantan Barat.

Etymology — From Latin, *forceps* (pincers) and the diminutive suffix *-ula*, hence *forcipula*, little pincers, in allusion to the shape of the individual staminate flowers.

Remarks — Vegetatively and well as by the staminate flower morphology this is one of the most distinctive species in the genus. In habitat *Bucephalandra forcipula* co-occurs with an undetermined member of the *Bucephalandra* Pygmaea Complex (known commercially as ‘Theia’) and an undescribed species of *Aridarum* Ridl.

Commercial names — ‘Gigante’.

11. *Bucephalandra gigantea* Bogner in Pl. Syst. Evol. 145: 159, fig. 1 & 2. 1984; Bogner & Hay in Telopea 9: 196. 2000. – Fig. 23K.

Holotype: Indonesian Borneo, Kalimantan Timur (“Central East Borneo”), Kabupaten Kutai Barat (“W. Koetai”), Kiau River, 25 Oct 1925, F. H. Endert 4580 (K!; isotypes: BO!, L!).

Description — See Bogner & Hay (2000: 196).

Ecology — *Bucephalandra gigantea* is rheophytic on rocks submerged in water and on small waterfalls, reported from c. 700 m above sea level. Endert (in sched.) reported *B. gigantea* as forming the dominant rheophytic vegetation.

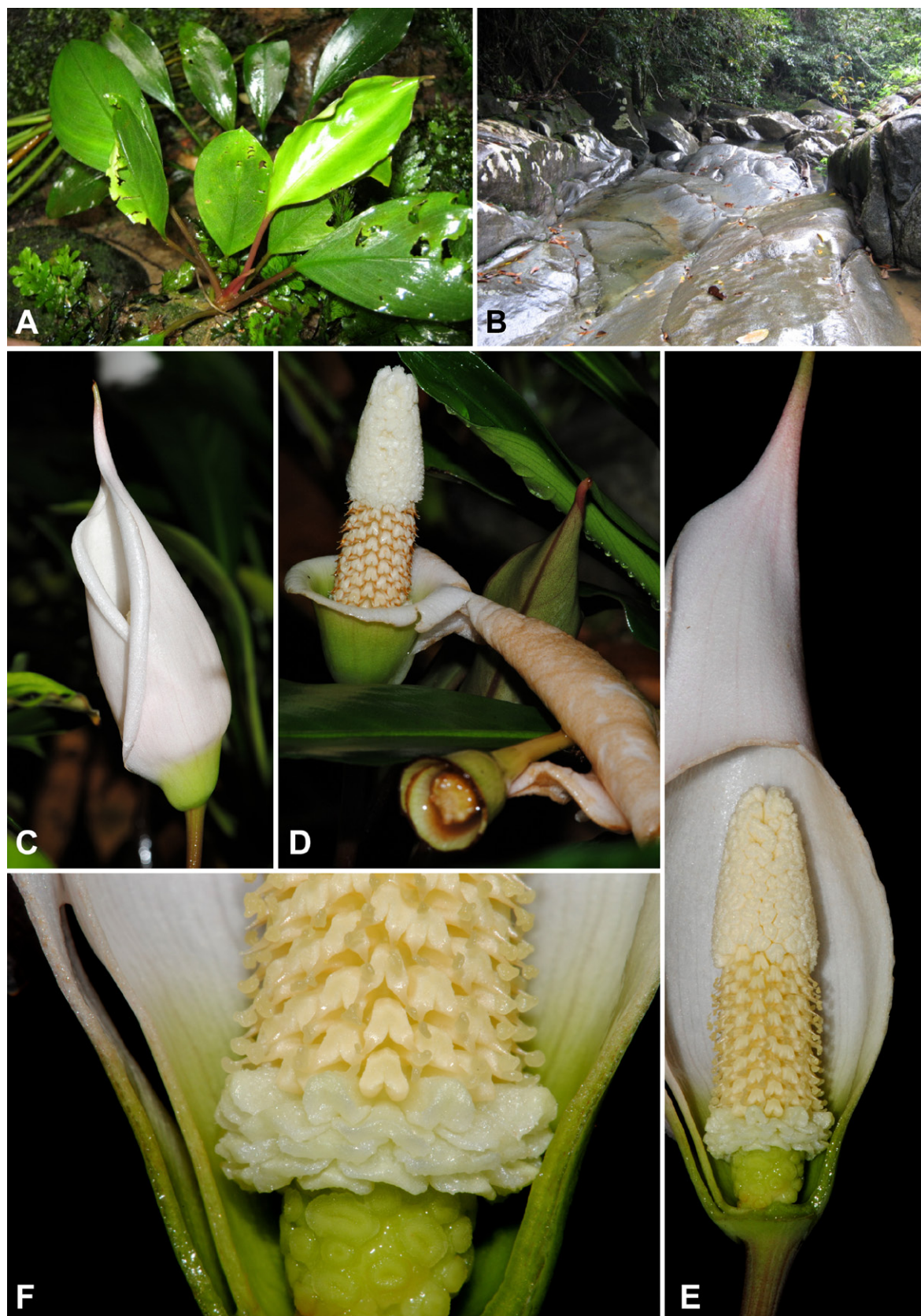


Fig. 9. *Bucephalandra forcipula* – A: plants in habitat; B: habitat; *B. forcipula* occurs along shaded margins of waterfall; C: inflorescence at pistillate anthesis; D: spadix at staminate anthesis, spathe limb nearly completely shed and beginning to degrade; a post-anthesis inflorescence is clearly visible; E: inflorescence at onset of staminate anthesis, nearside spathe artificially removed; F: detail of staminate flower zone and reflexed interstice staminodes at staminate anthesis. – Photographs: from K. Nakamoto AR-3772; A & B by K. Nakamoto; C–F by P. C. Boyce.

Distribution — So far known only from the type locality, where it is described as “very common here, forming the vegetation” (Endert in sched., translated from Dutch).

Remarks — *Bucephalandra gigantea* is presently the largest described *Bucephalandra* species, remarkable for the size of the leaf blades. The Kew isotype has the most complete field data, and there it is noted “andere bijzonderheden” (other observations) “already a few specimens collected along the rivulets but much smaller there”. Neither of the published descriptions (Bogner 1984; Bogner & Hay 2000) makes mention of any colours, although the label on the Kew isotype records “petioles reddish, leaf upper surface blotched/spotted reddish; ... spathe pink; ... fruit green” (translated from Dutch).

Commercial names — None.

12. *Bucephalandra goliath* S. Y. Wong & P. C. Boyce, **sp. nov.** – Fig. 10 & 23L.

Holotype: Indonesian Borneo, Kalimantan Barat, Kabupaten Melawi, Kecamatan Nanga Pinoh, Jalan 28, 8 km E of Kampong Nyangai, Landau Garong, logging road 25 km S of Nanga Pinoh, Ulu Sungai Reret and Ulu Sungai Sentulang, 00°34'31.9"S, 111°56'30.8"E, 16 Oct 2012, K. Nakamoto AR-4040 (BO!; isotypes: SAR!, SBC!, SING!).

Diagnosis — The leaf blades of *Bucephalandra goliath* are most similar to those of *B. ultramafica*, but *B. goliath* differs from *B. ultramafica* in its overall habit, having considerably elongated pendent naked stout stems. The spadix of *B. goliath* is notable by the bluntly cylindrical appendix clothed with large staminodes, and by the different morphology of the staminate flowers as compared with *B. ultramafica*.

Description — Robust erect to pendulous obligate rheophytic herbs up to 15 cm tall but occurring as pendent masses to over 1 m long. *Stem* initially erect and obscured by sheathing leaf bases, later (on old plants), mostly naked with tufts of leaves at tips, stems pendulous to 50 cm or more with active tips ascending, older stems branching repeatedly to form curtains hanging for 1 m or more. *Leaves* in tufts of 10 or more at tips of active shoots; *petiole* 5–6 cm long × c. 2.5 mm in diam., longitudinally ridged, adaxially canaliculate, reddish brown, sheathing at extreme base, wings extended into a very narrowly triangular ligular portion to 4 cm long; *blade* narrowly elliptic, 10–15 cm long × 1–1.5 cm wide, rather thickly coriaceous, semi-glossy medium green adaxially, pale yellow-green abaxially, base cuneate, apex acute to slightly acuminate, apiculate for c. 1.5 mm, margin usually straight and slightly recurved; *midrib* abaxially and particularly adaxially prominent, red abaxially; *primary lateral veins* c. 4 on each side, diverging at c. 30° and

running to a marginal vein; *interprimary veins* alternating with primaries and scarcely differentiated; *secondary venation* adaxially ± obscure, abaxially fine and ± following line of interprimaries; *tertiary venation* obscure. *Inflorescence* solitary, very seldom 2 together separated by a prophyll; *peduncle* exceeding petioles, 4.5–8 cm long × c. 2 mm in diam., somewhat compressed, conspicuously longitudinally sulcate, pale red, with distal-most expanded portion below spathe medium green. *Spathe* ovate, not constricted, 3.5–5.5 cm long; *lower spathe* funnel-form, green, persistent; *limb* inflating at pistillate anthesis, gaping to produce a narrow slit-like opening along upper ⅔ of spathe limb, caducous by fragmenting into large semi-coherent pieces at staminate anthesis, white, apiculate for c. 2 mm. *Spadix* 2–3.5 cm long; *pistillate zone* 4–5 mm long × c. 3 mm in diam., with c. 4 spirals of pistils; *pistils* rhombic-globose, c. 0.5 mm in diam., milky green; *stigma* sessile, capitate, c. ½ diameter of ovary, papillate at anthesis; *pistillodes* absent; *interstice* with c. 2 rows of *scale-like staminodes*, these c. 2 mm long × c. 2.5 mm wide, distal margin thickened and upward curving, staminodes initially erect, then spreading, white, later (post-anthesis) becoming green and persisting to cover developing fruit; *staminate zone* 5–6 mm long × c. 5 mm in diam., consisting of c. 4 rows of flowers; *staminate flowers* cream; *stamen* comparatively large, c. 1 mm across; *filament* conspicuous; *connective* gibbose strap-shaped; *thecae* inserted ventrally, ellipsoid, c. 1 mm long × c. 0.5 mm wide, smooth; *thecae horns* equalling associated theca, base areole-like, horn very short, spreading; *appendix* bluntly cylindrical, base abruptly tapering into staminate zone, 1.5–2 cm long × 6–7 mm in diam., cream to medium yellow; *appendix staminodes* obpyramidal, truncate, 2–3 mm in diam., upper surface smooth and slightly glossy. *Fruiting spathe* not seen.

Ecology — *Bucephalandra goliath* occurs on granite waterfalls under perhumid lower hill forest at c. 250 m above sea level.

Distribution — So far known only from the area of Nanga Pinoh and Nanga Taman, where it is scattered and highly localized.

Etymology — Derived from Goliath of Gath (one of five city states of the Philistines), the giant Philistine warrior, and used in allusion to the robust and large stature of this species.

Remarks — The long stout pendent stems forming dense curtains of growth are immediately diagnostic. The leaf blade is also highly distinctive, although the leaf blades of Sabah *Bucephalandra ultramafica* are superficially similar.

Commercial names — ‘Goliath’, ‘Goliathe’, ‘Jupiter’.

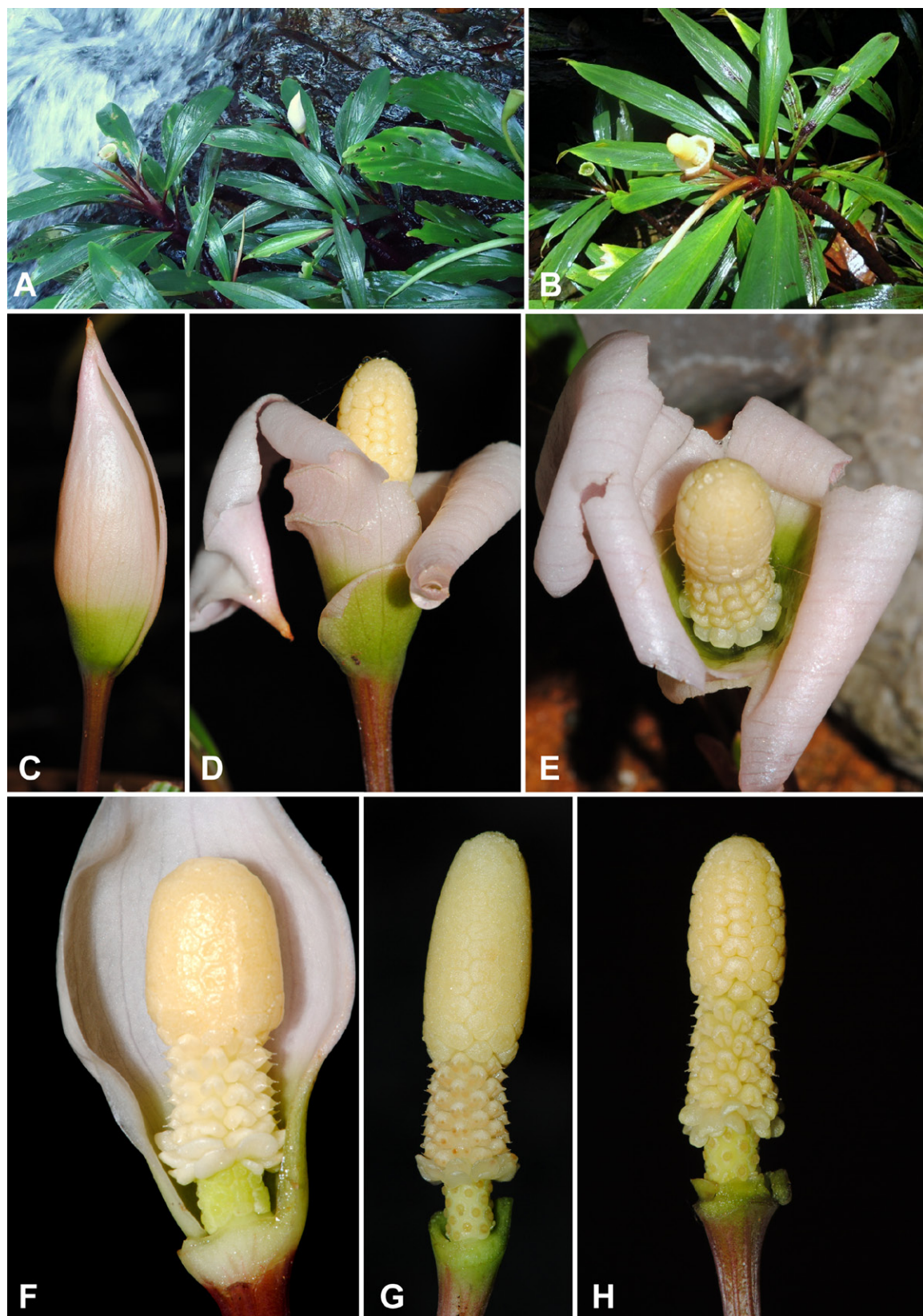


Fig. 10. *Bucephalandra goliath* – A & B: plants in habitat; note (B) long, naked stem; C: inflorescence at early pistillate anthesis; D & E: inflorescence at onset of staminate anthesis with spathe limb beginning to shed in separate pieces; F: spadix at staminate anthesis, spathe limb and nearside part of lower spathe artificially removed; note that interstice staminodes are beginning to lower; G & H: spadix at onset of staminate anthesis, spathe artificially removed; note that interstice staminodes are beginning to lower. – Photographs: A from K. Nakamoto AR-3929; B–E, G & H from K. Nakamoto AR-3848; F from K. Nakamoto AR-4040; A & B by K. Nakamoto; C–H by P. C. Boyce.

Additional specimens seen (paratypes) — **INDONESIAN BORNEO: KALIMANTAN BARAT:** Kabupaten Sekadau, Kecamatan Nanga Taman, environs of Nanga Taman, 4 Apr 2012, *K. Nakamoto AR-3848* (BO!; SAR!); *ibid.*, 22 May 2012, *K. Nakamoto AR-3929* (BO!, SAR!).

13. *Bucephalandra kerangas* S. Y. Wong & P. C. Boyce, **sp. nov.** – Fig. 11 & 23M.

Holotype: Malaysian Borneo, Sarawak, Bahagian Samarahan, Simumjan District, Sebuyau, logging road at Sabal, 7 Feb 1995, *Runi ak Punga & al. S.71313* (SAR!; isotypes: K!, KEP!, L!, MO!, SAN).

Diagnosis — The spadix of *Bucephalandra kerangas* is somewhat reminiscent of that of *B. elliptica*, although readily differentiated by the abrupt transition into the narrowly cylindrical staminate flower zone, with the base of the appendix truncate, and by the excavated, extended staminodes at the appendix tip. Ecologically *B. kerangas* is unique in the genus (indeed, in the entire *Schismatoglottideae*) by being restricted to kerangas.

Description — Small solitary obligate rheophytic herbs to c. 13 cm tall, but in exposed situations only c. ½ this height. *Stem* creeping and rooting, c. 1 cm in diam., with active portion sub-erect. *Leaves* c. 10 together, semi-erect; *petiole* 2–4 cm long × c. 2 mm in diam., adaxially canaliculate, conspicuously longitudinally ribbed, dark reddish brown, sheathing at extreme base, wings extended into a very narrowly triangular ligular portion to 4 cm long; *blade* lanceolate, 6–12 cm long × 1–4 cm wide, stiffly to moderately coriaceous, semi-glossy deep green adaxially, paler and yellowish pink to reddish green abaxially, base cuneate, apex acute, apiculate for c. 2.5 mm, straight and somewhat reflexed, especially in plants from exposed situations; *midrib* abaxially and adaxially prominent, abaxially with at least basal ½ ridged; *primary lateral* and *interprimary veins* not differentiated, together totalling c. 4 per side, diverging at c. 30° and running to a marginal vein; *secondary venation* adaxially ± obscure, abaxially fine; *tertiary venation* adaxially obscure, forming a faint tessellate reticulum. *Inflorescence* solitary; *peduncle* exceeding petioles, 5–6 cm long × c. 1.5 mm in diam., conspicuously longitudinally sulcate, reddish green with ridges darker red. *Spathe* broadly ellipsoid, not constricted, c. 3.7 cm long; *lower spathe* funnel-form, green, persistent; *limb* gaping, then caducous, white shading to green at junction with lower persistent spathe, limb acuminate for c. 1 cm and apiculate for c. 4 mm, apiculum green. *Spadix* 2–2.5 cm long; *pistillate zone* c. 5 mm long × c. 3 mm in diam., with c. 3 spirals of pistils; *pistils* rhombic-globose, c. 0.5 mm in diam., bright green; *stigma* sessile, umbonate, c. ½ diameter of ovary, producing a conspicuous meniscus-like droplet at anthesis, later (post-anthesis) sunken centrally; *pistillodes* 2–4 at base

of pistillate zone, tongue-shaped, c. 0.5 mm long and wide, waxy white; *interstice* with 2 rows of *scale-like staminodes*, these c. 2 mm long × 1.5 mm wide, ventrally gibbose, margin spathulate, basally green, apically white, erect during pistillate anthesis, reflexing prior to staminate anthesis, later (post-anthesis) becoming green and persisting to cover developing fruit; *staminate zone* c. 5 mm long × c. 4 mm in diam., consisting of c. 4 rows of flowers; *staminate flowers* ascending to display almost entire ventral surface, creamy yellow to pinkish cream; *stamen* comparatively large, c. 2 mm long; *filament* small, stout; *connective* strap-shaped; *thecae* inserted ventrally, ellipsoid, c. 1 mm long × c. 0.5 mm wide, smooth; *thecae horns* c. ¼ length of associated theca, setaceous, outward-pointing; *appendix* bullet-shaped, base abruptly truncate at junction with staminate flower zone, 1–1.5 cm long × c. 5 mm in diam., cream; *appendix staminodes* tending to form groups of 3 or 4, obpyramidal, tops irregularly polygonal, truncate, 0.5–1 mm in diam., smooth and somewhat glossy, cream. *Infructescences* not seen.

Ecology — *Bucephalandra kerangas* is rheophytic on whitish sandstone rocks and waterfalls along oligotrophic streams under open lowland to lower hill kerangas (tropical heath-forest) at 25–360 m above sea level.

Distribution — N and S flanks of the C part of the Klingkang Range, Sarawak (Bahagian Sri Aman) & Kalimantan Barat (Kabupaten Sanggau).

Etymology — *Kerangas* is derived from the name of the vegetation, tropical heath-forest, to which this new species is restricted. The word *kerangas*, translates as “land that cannot grow rice”, and is from the Iban language.

Remarks — The only *Bucephalandra* species so far known to occur in *kerangas*, a habitat not usually favouring rheophytes. Plants in exposed situations tend to be dwarfed, with stiffly coriaceous leaf blades and with the margins noticeably recurved, as compared with plants in shade, which are inclined to be larger, with softer-textured arching leaf blades. When brought into cultivation these exposed-situation plants grow on to resemble the shade-dwelling individuals.

Commercial names — None.

Additional specimens seen (paratypes) — **MALAYSIAN BORNEO: SARAWAK:** Bahagian Sri Aman: Tempat Perkelahan Tapang Rumput, 01°04'13.0"N, 111°17'35.7"E, 23 Aug 2009, *P. C. Boyce & S. Y. Wong AR-2595* (SAR!, SBC!, SING!). — **INDONESIAN BORNEO: KALIMANTAN BARAT:** Kabupaten Kapuas Hulu, Kecamatan Badau, Wong Garai, 15 km NW of Badau, 00°58'13.0"N, 111°49'30.3"E, 17 May 2013, *K. Nakamoto AR-4145* (BO!, SAR!, SBC!, SING!).

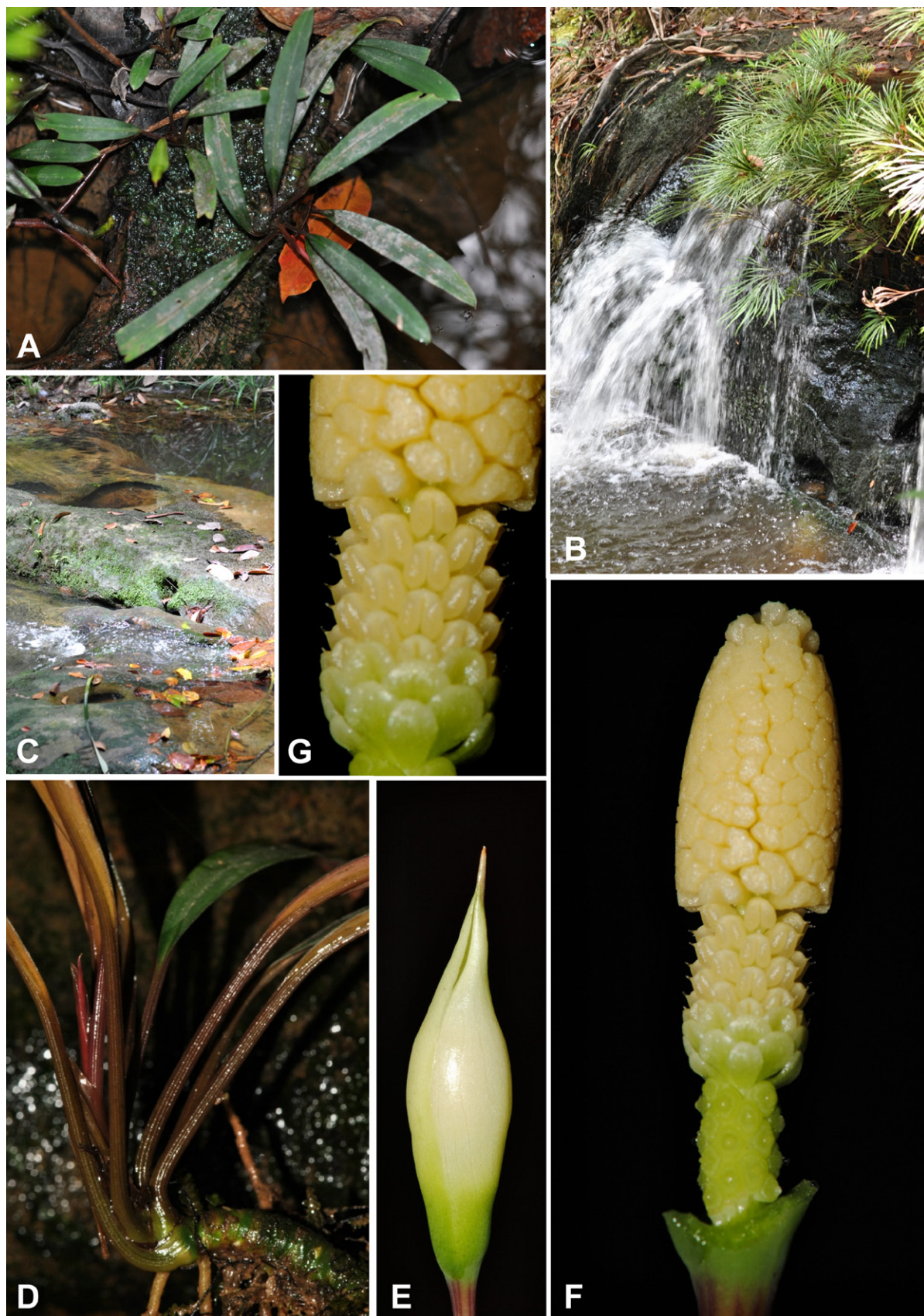


Fig. 11. *Bucephalandra kerangas* – A: plant in habitat; B & C: habitat; D: detail of plant; note creeping rhizome-like stem and longitudinally sulcate petioles; E: inflorescence at pistillate anthesis; F: inflorescence at pistillate anthesis, spathe artificially removed; G: detail of spadix at pistillate anthesis, note interstice staminodes and staminate flower thecae are erect. – Photographs: from P. C. Boyce & S. Y. Wong AR-2595; all by P. C. Boyce.

14. *Bucephalandra kishii* S. Y. Wong & P. C. Boyce, sp. nov. – Fig. 12 & 23N.

Holotype: Indonesian Borneo, Kalimantan Barat, Kabupaten Melawi, Kecamatan Nanga Taman, Kampung Entebah, Gunung Saran, 00°25'24"S, 111°17'42"E, 1500 m, 25 Aug 2012, K. Nakamoto AR-4019 (BO!; isotypes: SAR!, SBC!, SING!).

Diagnosis — *Bucephalandra kishii* is immediately recognizable by the erect stem with regular rosettes of leaves and by the leaf blades adaxially with prominently raised primary lateral veins; in these characters alone *B. kishii* cannot be confounded with any other *Bucephalandra* species. *Bucephalandra kishii* is further exemplified by the conic appendix comprised of lax elongate staminodes with excavate tips.

Description — Small obligate or facultative rheophytic herbs to 12 cm tall. *Stem* erect, mostly obscured by sheathing leaf bases c. 1 cm in diam. *Leaves* many together in a dense to rather loose rosette; *petiole* 1–3.5 cm long × c. 2 mm in diam., adaxially canaliculate, green or deep reddish black, or purple, sheathing at extreme base, wings extended into a very narrowly triangular ligular portion to 3 cm long; *blade* elliptic to ovate, 2.5–5 cm long × 1.5–2 cm wide, rather thickly coriaceous, semi-glossy medium green to very dark reddish black or purple-green adaxially, paler greenish red or green abaxially, base cuneate, apex rounded and apiculate for c. 1.5 mm, margin undulate to almost crispulate; *midrib* abaxially very prominent, adaxially prominent; *primary lateral veins* 3 or 4 on each side, very prominent adaxially, flush with blade or almost so abaxially, diverging at c. 45° and running to an adaxially strong marginal vein; *interprimary veins* much less defined adaxially, almost flush with blade abaxially; *secondary venation* abaxially forming a faint tessellate reticulum. *Inflorescences* several together alternating with a foliage leaf and/or a conspicuous prophyll; *peduncle* exceeding petioles, 5–9 cm long, conspicuously longitudinally ribbed, medium to dark green or red, or deep red-black. *Spathe* broadly ovate, becoming inflated turbinate just prior to anthesis, not constricted, 3.5–5 cm long, with acuminate part c. 1 cm long; *lower spathe* funnel-form, pale yellow, pale pink, or red-flushed, persistent; *limb* inflating in middle with a slit appearing on distal acuminate and inflated portion, then caducous, white, or pale to medium pink, apiculate for c. 2 mm. *Spadix* 2–2.5 cm long; *pistillate zone* 7–9 mm long × c. 3 mm in diam., with 4 or 5 spirals of pistils; *pistils* compressed globose, c. 0.5 mm in diam., lime-green; stigma sessile, capitate, c. ½ diameter of ovary, papillate at anthesis; *pistillodes* 2–4 at base of pistillate zone, clavate with flat top, c. 0.5 mm in diam., white; *interstice* with c. 2 rows of scale-like staminodes, these c. 2 mm long × c. 2 mm wide, distally notched, at pistillate anthesis erect then at staminate anthesis reflexing, white; *staminate zone*

weakly conic, 7–9 mm long × c. 6 mm in diam. at base and c. 4 mm in diam. at apex, consisting of 8 or 9 regular rows of flowers; *staminate flowers* waxy white; *stamen* comparatively large, c. 2.5 mm long × c. 1 mm across; *filament* triangular-rostrate, ascending; *thecae* inserted ventrally, narrowly ellipsoid, c. 1 mm long × c. 0.3 mm wide, smooth; *thecae horns* equalling associated theca, setaceous, upward curving; *appendix* bullet-shaped, shortly stipitate, abruptly and widely truncate at junction with staminate flowers, lowermost staminodes of appendix overhanging and partially obscuring uppermost stamens; appendix 1.7–2.3 cm long × c. 12 mm in diam., waxy white; *appendix staminodes* slender obpyramidal, tops somewhat to deeply excavate, 0.5–1 mm in diam. *Fruiting spathe* funnel-form, c. 1 cm in diam., with shield-shaped staminodes persistent, turning green, spent distal part of spadix falling; *fruits* and *seeds* not seen.

Ecology — *Bucephalandra kishii* occurs on riversides under open-canopied upper hill forest over granite, at and above 1500 m above sea level. The species appears to be a facultative rather than obligate rheophyte.

Distribution — Restricted to Gunung Saran.

Eponymy — Named for Hiroyuki Kishi, ardent collector and skilled grower of aquarium plants.

Remarks — In having leaf blades with the primary lateral veins adaxially conspicuously raised this highly distinctive species is reminiscent of juvenile plants of the *Aridarum Burtii* Complex, although the inflorescences are quite different.

In wild populations there is considerable variation in leaf blade colour, and plants with deep red or deep red-black leaf blades have pink spathes, whereas plants with green leaf blades have white spathes. The individuals with red-black leaves and pink inflorescences are highly ornamental.

Commercial name — ‘Achilles’, ‘Black Skeleton’ and ‘Green Skeleton’.

Additional specimens seen (paratypes) — INDONESIA BORNEO: KALIMANTAN BARAT: Kabupaten Melawi, Kecamatan Nanga Taman, Kampung Entebah, Gunung Saran, 00°25'24"S, 111°17'42"E, 25 Aug 2012, K. Nakamoto AR-4005 (BO!, SAR!, SBC!, SING!), K. Nakamoto AR-4008 (BO!, SAR!, SBC!, SING!), K. Nakamoto AR-4010 (BO!, SAR!, SBC!, SING!) & K. Nakamoto AR-4011 (BO!, SAR!, SBC!, SING!).

15. *Bucephalandra magnifolia* H. Okada & Y. Mori in Acta Phytotax. Geobot. 51: 4, fig. 2 & 4B. 2000. – Fig. 23O.

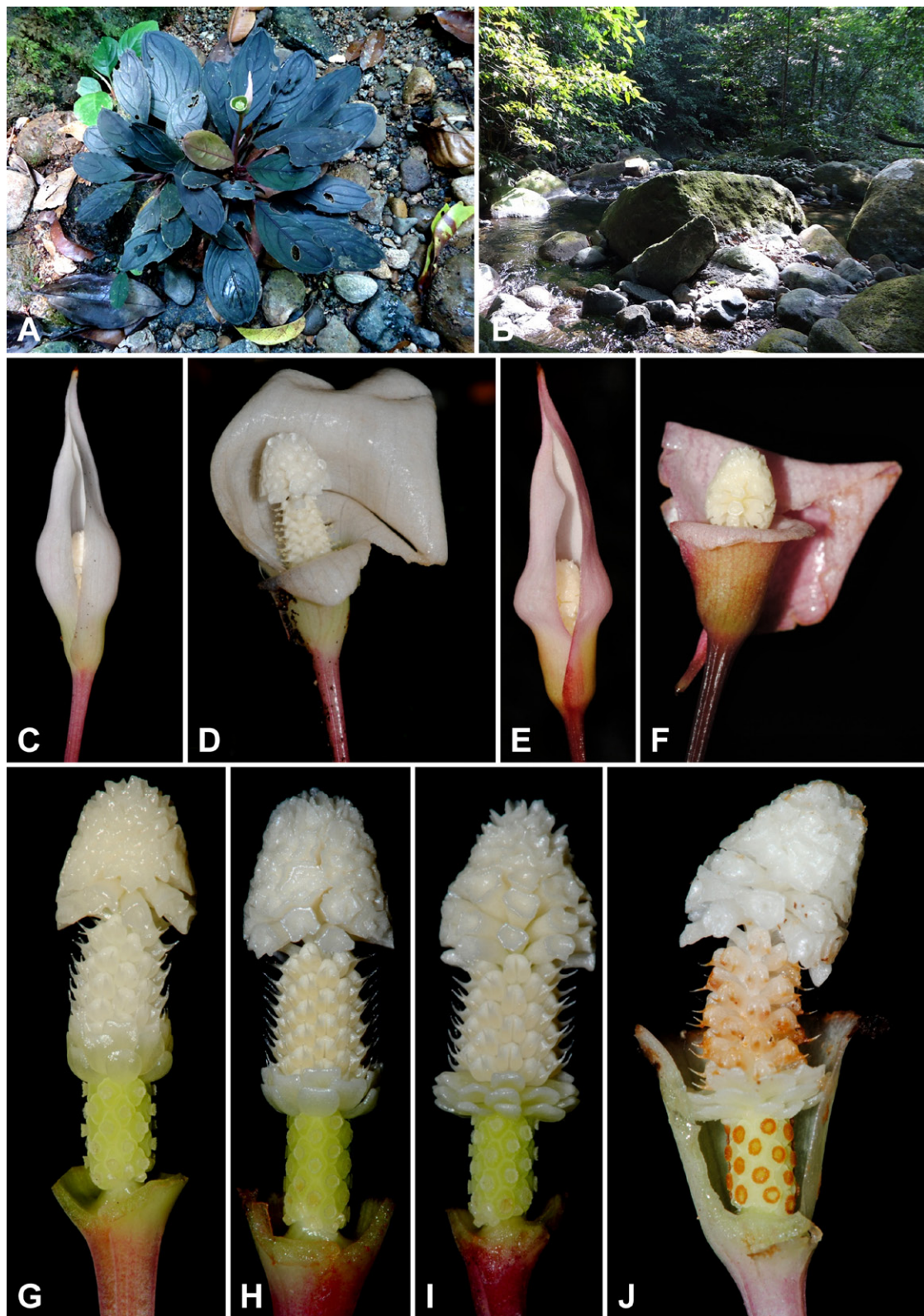


Fig. 12. *Bucephalandra kishii* – A: plant in habitat; B: habitat; *B. kishii* occurs along shaded margins of waterfall; C & E: inflorescence at pistillate anthesis; D & F: inflorescence at staminate anthesis, spathe limb beginning to shed; G: spadix at pistillate anthesis, spathe artificially removed; note erect interstice staminodes and staminate flower thecae; H: spadix at onset of staminate anthesis, spathe artificially removed; note interstice staminodes and staminate flower thecae are beginning to reflex; I: spadix at staminate anthesis, spathe artificially removed; note interstice staminodes and staminate flower thecae are fully reflexed; J: spadix post-anthesis, spathe limb shed naturally, nearside of lower spathe artificially removed; note colour changes to stigmas and thecae horns. – Photographs: A, B & I from K. Nakamoto AR-4055; C, D & H from K. Nakamoto AR-4019; E & F from K. Nakamoto AR-4011; G & J from K. Nakamoto AR-4010; A & B by K. Nakamoto; C–J by P. C. Boyce.

Holotype: Indonesian Borneo, Kalimantan Utara (“East Kalimantan”), Kabupaten Nunukan (“Bulungan”), Kecamatan Krayan, Long Bawan, Gunung Malim, 03°55'N, 115°40'E (estimated from Google Earth), 11 Sep 1990, *H. Okada & D. Komara 5024* (TI!; isotype: BO!).

Description — See Okada & Mori (2000: 4–7, fig. 2).

Ecology — *Bucephalandra magnifolia* occurs as a rheophyte on sedimentary riverside rocks under upper hill to lower montane forest, between 980–1300 m above sea level.

Distribution — Known with certainty from Long Bawan (but see below).

Remarks — Plants very possibly this species from further east (Kabupaten Malinau, Kalimantan Utara) are in cultivation but have yet to flower to confirm determination.

Commercial names — None.

Additional specimens seen — INDONESIA BORNEO: KALIMANTAN UTARA: Kabupaten Nunukan, Krayan Kecamatan, between Pa Patar & Pa Mani, 29 Sep 1990, *H. Okada & J. Murata 25266* (BO!, TI!).

16. *Bucephalandra minotaur* S. Y. Wong & P. C. Boyce, **sp. nov.** – Fig. 13 & 23P.

Holotype: Indonesian Borneo, Kalimantan Barat, Sekadau/Melawi regencies boundary, 115 km S of Nanga Pinoh, 00°58'21.8"S, 111°30'54.4"E (estimated from Google Earth), 22 May 2012, *K. Nakamoto AR-3951* (BO!; isotypes: SAR!, SBC!, SING!).

Diagnosis — *Bucephalandra minotaur* is distinguished from all other species of *Bucephalandra* by staminate flowers with thecae horns much shorter than the thecae, the sinus between the thecae not or only barely extending to the front of the staminate flower, and the staminodes of the lower 1/3 of the appendix flat and morphologically identical to those of the upper appendix.

Description — Small obligate rheophytic herbs to 20 cm tall. *Stem* erect, older plants with stem shortly creeping and with active portion sub-erect, c. 1 cm in diam. *Leaves* many together; *petiole* 6–8 cm long × c. 1.5 mm in diam., weakly longitudinally ridged, adaxially canaliculate, reddish green, sheathing at extreme base, wings extended into a very narrowly triangular ligular portion to 4 cm long; *blade* lanceolate, somewhat oblique, 9–11 cm long × 1–1.5 cm wide, coriaceous, matte dark green adaxially, lighter green abaxially, base sub-cuneate, apex acute to acuminate, apiculate for c. 1.5 mm, margin undulate; *midrib* abaxially and adaxially prominent, tending to be reddish abaxially; *primary lateral veins* c. 3 on each side,

diverging at c. 40° and running to a marginal vein; *interprimary veins* very faint; *secondary venation* adaxially ± obscure, abaxially somewhat raised; *tertiary venation* obscure. *Inflorescence* solitary; *peduncle* exceeding petioles, 9–12 cm long, stout, c. 4 mm in diam., somewhat angled and weakly longitudinally sulcate, bright reddish shading to green at lower spathe. *Spathe* oblong-ovate, not constricted, 5–6 cm long; *lower spathe* narrowly funnel-form, green, persistent; *limb* inflating at pistillate anthesis and gaping along most of its length, opening wide at staminate anthesis, then caducous, ivory, apiculate for c. 2 mm, apiculum green. *Spadix* 4–5 cm long; *pistillate zone* 5–6 mm long × c. 3 mm in diam., with 2–5 spirals of pistils; *pistils* rhombic-globose, c. 0.6 mm in diam., pale yellow-green; *stigma* sessile, umbonate, c. 1/2 diameter of ovary, slightly depressed, papillate at anthesis, later (post-anthesis) sunken centrally; *pistillodes* 2–4 at base of pistillate zone, tongue-like with a clavate tip, c. 0.3 mm long, white with tip yellow; *interstice* with 2 or 3 rows of *scale-like staminodes*, these c. 3 mm long × c. 1 mm wide, bases thickened, staminodes initially erect, then spreading, initially white, later (post-anthesis) becoming green and persisting to cover developing fruit; *staminate zone* 8–11 mm long × 4–6 mm in diam., consisting of 5–11 rows of flowers; *staminate flowers* initially spreading, reflexing at staminate anthesis to present thecae horns, creamy white; *stamen* large, c. 2 mm across; *filament* slender; *connective* semi-terete, dorsally rounded, ventrally flattened; *thecae* inserted ventrally, ellipsoid, c. 1 mm long × c. 0.5 mm wide, smooth; *thecae* horns very short, c. 0.2 mm long, upward-turned; *appendix* bluntly cylindrical to slightly fusiform, 2–3 cm long × c. 6 mm in diam., cream; *appendix staminodes* obpyramidal, rather regularly polygonal, lowermost staminodes c. 2 mm in diam., uppermost c. 1/2 this size, tops truncate, smooth. *Fruiting spathe* narrowly funnel-form, c. 1 cm in diam.; *fruits* and *seeds* not seen.

Ecology — *Bucephalandra minotaur* occurs as a rheophyte on the Cretaceous granites of the Schwaner Range, at c. 165 m above sea level.

Distribution — Known only from the type locality.

Etymology — From Latin, *Minotaurus* (from Greek, *Minotavros*), the Minotaur of Greek myth, a monster with the head of a bull and the body of a man, the epithet here coined to reflect the staminate flowers reflexing at staminate anthesis each to resemble a bull charging head-down.

Remarks — *Bucephalandra minotaur* occurs along the flanks of the Schwaner Range, within an area of quite extraordinary biological diversity, where it co-occurs with numerous undescribed species of aroids, and doubtless other undescribed species, too.

Commercial names — ‘Gigant’.

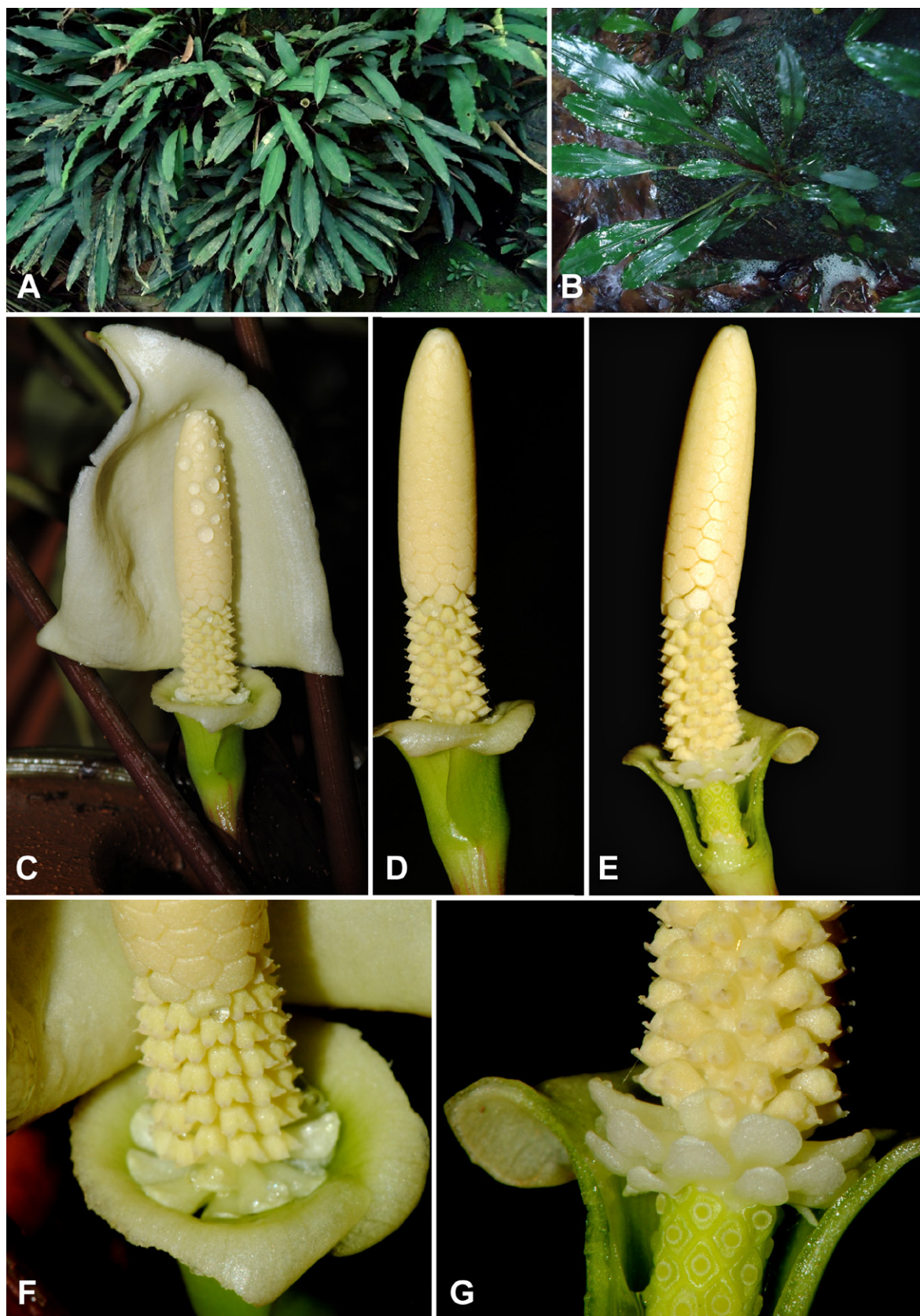


Fig. 13. *Bucephalandra minotaur* – A & B: plants in habitat; C: inflorescence at staminate anthesis, with spathe limb nearly shed; D: inflorescence at staminate anthesis, spathe limb shed; E: inflorescence at staminate anthesis, spathe limb fallen naturally, nearside part of lower spathe removed artificially; note that interstice staminodes have reflexed to close entrance of lower spathe; F: detail of interstice staminodes sealing lower spathe; G: detail of lower spathe and fertile portions of staminate phase spadix, nearside part of spathe artificially removed. – Photographs: from K. Nakamoto AR-3951; A & B by K. Nakamoto; C–G by P. C. Boyce.

17. *Bucephalandra motleyana* Schott, Gen. Aroid.: t. 56. 1858; Prodr. Syst. Aroid.: 319. 1860; Engl., Monogr. Phan. 2: 354. 1879; Nat. Pflanzenfam. 2(3): 132. 1889; Pflanzenr. 55 (IV.23Da): 122, fig. 74. 1912.

Holotype: Indonesian Borneo, Kalimantan Selatan (?), *J. Motley 404* (K!).

Description — Schott's original description (Schott 1858) is scanty and contains serious errors (see Bogner 1980 for discussion). Subsequent descriptions (Bogner 1980; Bogner & Hay 2000) are compiled from numerous different species, in line with then taxonomic concepts, and are therefore not reliable for envisaging *Bucephalandra motleyana*. Recollection of *B. motleyana* at the type locality is required, but see below.

Ecology — Unknown, but very probably rheophytic. It is of interest to mention that the bulk of the Meratus Range, from where *Bucephalandra motleyana* very probably originates, are ultramafic with outcrops of granite.

Distribution — Most likely collected from the S part of the Meratus Mountains (modern Kalimantan Selatan), but this requires confirmation on the ground.

Remarks — Notwithstanding almost universal application of the name *Bucephalandra motleyana* to *Bucephalandra* plants in herbaria, in literature, in living collections, and on the internet, we have not seen any plants, living, preserved, or depicted, that match Motley's original collection. While it is not 100% certain where Motley's collection was made, based on his known collection activities it very probably originated from the Meratus Mountains, in present-day Kalimantan Selatan.

James Motley was from 1854 superintendent of the Julia Hermina coal mine at Kalangan, modern Kalimantan Selatan. During this time, as he had from Labuan, Motley sent plant material, including living aroids, to Europe. Motley, his wife, and three children were murdered at Kalangan on 1 May 1859 during a local uprising at the start of the Bandjarmasin War (Walker 2005).

Bogner (1980) showed conclusively that the plate accompanying Schott's description (Schott 1858) contains serious inaccuracies. Uncorrected portions of Schott's plate were reproduced by Engler (1912). See Bogner (1980) and Boyce & Wong (2012) for discussion.

Commercial names — None.

18. *Bucephalandra muluensis* (M. Hotta) S. Y. Wong & P. C. Boyce, **comb. nov.** \equiv *Microcasia muluensis* M. Hotta in Mem. Coll. Sci. Kyoto Imp. Univ., Ser. B, Biol. 32(1): 20, fig. 1A–F. 1965. – Fig. 14 & 24B.

Holotype: Malaysian Borneo, Sarawak, Bahagian Miri ("4th Divn"), along Sungai Payau from Sungai Melinau

Paku to Rubang Payau, foot of Gunung Mulu, 22 Mar 1964, *M. Hotta 15329* (KYO!).

Description — Small obligate rheophytic herbs to 10 cm tall. *Stem* initially erect, later creeping with active portion sub-erect, c. 5 mm in diam. *Leaves* several together; *petiole* 2–3 cm long \times c. 1.5 mm in diam., adaxially canaliculate, bright green, sheathing at extreme base, wings extended into a very narrowly triangular ligular portion to 1 cm long; *blade* ovate to broadly elliptic, 2–4 cm long \times 1.5–2 cm wide, thinly coriaceous, weakly glossy bright green, slightly paler abaxially, base rounded to rounded-cuneate, apex acute and apiculate for c. 2 mm, margin flat; *midrib* abaxially and adaxially sharply prominent; *primary lateral veins* 3 or 4 on each side, diverging at c. 40° and running to a weak marginal vein; *interprimary veins* very weak; all other venation obscure. *Inflorescence(s)* solitary to up to 3 together interspersed with prophylls; *peduncle* exceeding petioles, c. 4 cm long, sub-terete, pale green. *Spathe* broadly ovate, not constricted, c. 3 cm long; *lower spathe* funnel-form, yellowish green, persistent; *limb* inflating and gaping distally at pistillate anthesis, then deliquescent-caducous during staminate anthesis, glistening white, apiculate for c. 2 mm, apiculum green. *Spadix* 1.3–1.5 cm long; *pistillate zone* c. 3 mm long \times c. 1.5 mm in diam., with c. 3 spirals of pistils; pistils rhombic-globose, c. 0.4 mm in diam., bright green; stigma sessile, umbonate, c. $\frac{2}{3}$ diameter of ovary, papillate at anthesis; *pistillodes* 2–4 at base of pistillate zone, bottle-shaped, c. 0.35 mm long., white, tip green; *interstice* with c. 2 rows of *scale-like staminodes*, these 1–2 mm long \times 0.8–1.5 mm wide, spatulate, initially erect, then spreading, initially matte white, later (post-anthesis) becoming green and persisting to cover developing fruit; *staminate zone* c. 3 mm long \times c. 2 mm in diam., consisting of c. 4 rows of flowers; *staminate flowers* medium yellow; *stamen* comparatively large, c. 1 mm across; *filament* short, slender; *connective* slender, prismatic; *thecae* inserted ventrally, ellipsoid, c. 1 mm long \times c. 0.4 mm wide, smooth; thecae horns sub-equalling associated theca, setaceous, spreading; *appendix* ellipsoid, basally somewhat abruptly transitioning to staminate flower zone, 7–9 mm long \times 3–4 mm in diam., medium yellow; *appendix staminodes* individually well-demarcated, obpyramidal, 0.5–1 mm in diam., upper surface brain-like with a central impression. *Fruiting spathe* funnel-form, c. 1 cm in diam., with shield-shaped staminodes persistent, turning green, spent distal part of spadix falling; *berry* depressed globose, 1–1.8 mm long \times 1–1.5 mm in diam., with numerous seeds, berries forming a hemispherical cluster protected by persistent staminodes, later pushed off and falling to reveal mature fruits.

Ecology — *Bucephalandra muluensis* is rheophytic on exposed to semi-shady karst limestone rocks along streams under perhumid to moist lowland forest, below 100 m above sea level.

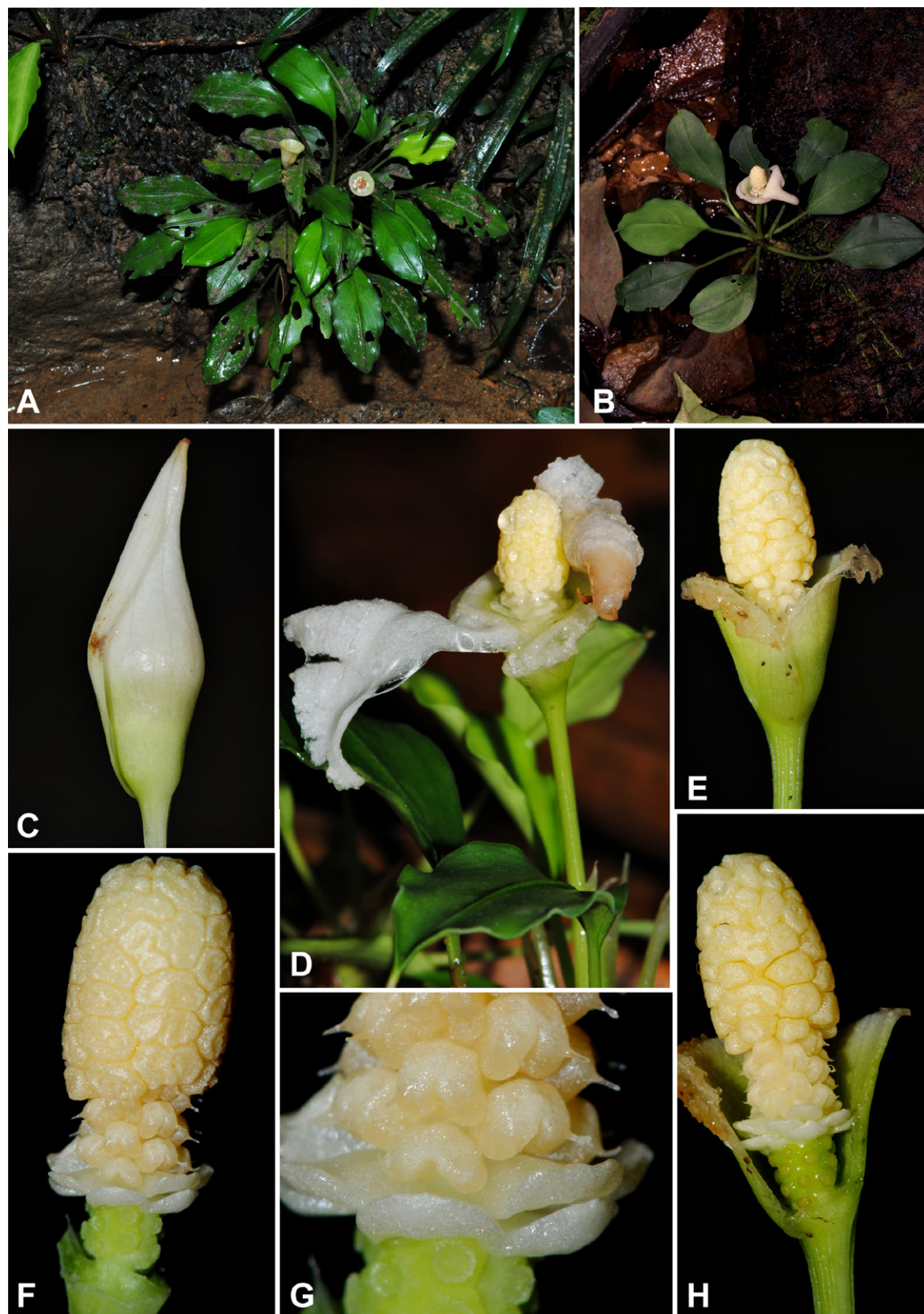


Fig. 14. *Bucephalandra muluensis* – A & B: plants in habitat; C: inflorescence at pistillate anthesis; D: inflorescence at staminate anthesis, spathe limb shedding; E: inflorescence at staminate anthesis, spathe limb fallen naturally; F: spadix at staminate anthesis; note reflexed interstice staminodes, reflexed thecae, and pollen droplet at tip of thecae horns; G: detail of staminate flowers and interstice staminodes; H: inflorescence at staminate anthesis, spathe limb fallen naturally, nearside part of lower spathe removed artificially; note that interstice staminodes have reflexed to close entrance of lower spathe. – Photographs: A, C, E–H from P. C. Boyce & S. Y. Wong AR-3813; B & D from P. C. Boyce & al. AR-1949; all by P. C. Boyce.

Distribution — Known only on the Mulu National Park limestones, where it is scattered and not common.

Remarks — *Bucephalandra muluensis* is one of two species present in Mulu National Park, the other is the more widespread *B. oblangceolata*. Aside from the morphological differences highlighted in the key to species, the Mulu species are also ecologically discrete, with *B. oblangceolata* restricted to shales and *B. muluensis* a limestone obligate.

Bucephalandra muluensis is readily identifiable even when not flowering owing to the bright green leaf blades.

Commercial names — None.

Additional specimens seen — MALAYSIAN BORNEO: SARAWAK: Bahagian Miri: Marudi, Long Lama, Mulu National Park, trail to Deer Cave, 04°02'02.0"N, 114°49'00.0"E, 6 Aug 2006, *P. C. Boyce & al. AR-1949* (SAR); Marudi, Long Lama, Mulu N.P., Long Langsat, Sungai Langsat, draining into the Sungai Tutoh, 04°01'12.4"N, 114°49'06.6"E, 13 Mar 2012, *P. C. Boyce & Wong Sin Yeng AR-3813* (SAR).

19. *Bucephalandra oblangceolata* (M. Hotta) S. Y. Wong & P. C. Boyce, **comb. nov.** ≡ *Microcasia oblangceolata* M. Hotta in Mem. Coll. Sci. Kyoto Imp. Univ., Ser. B, Biol. 32(1): 21, fig. 1G–M. 1965. – Fig. 15 & 24C. Holotype: Brunei Darussalam, Temburong Prov., vicinity of Labu, Bukit Peradayan, 25 Jan 1964, *M. Hotta 13586* (KYO!; isotypes: L!, SAR!).

Description — Small obligate rheophytic herbs to 60 cm tall. *Stem* erect, older plants with stem shortly creeping and with active portion sub-erect, c. 1.5 cm in diam. *Leaves* many together, erect; *petiole* 4–6 cm long × c. 1.7 mm in diam., weakly longitudinally ridged, adaxially canalliculate, dark reddish brown, sheathing at extreme base, wings extended into a very narrowly triangular ligular portion to 4 cm long; *blade* narrowly lanceolate to narrowly elliptic, 10–14 cm long × 1–2 cm wide, coriaceous, semi-glossy dark green adaxially, lighter green abaxially, base sub-cuneate, apex acute to acuminate, apiculate for c. 1.5 mm, margin undulate; *midrib* abaxially and adaxially somewhat prominent, reddish abaxially; *primary lateral* and *interprimary veins* very faint; *secondary venation* adaxially ± obscure; *tertiary venation* obscure. *Inflorescence* solitary; *peduncle* exceeding petioles, 8–10 cm long × c. 1.5 mm in diam., conspicuously longitudinally sulcate and reddish with ridges deeper red. *Spathe* oblong-ovate, not constricted 3.5–4 cm long; *lower spathe* funnel-form, medium green, persistent; *limb* inflating at pistillate anthesis, gaping to produce a longitudinal slit to about edge of lower spathe, limb reflexing at staminate anthesis, then somewhat deliquescent along margins, caducous, white, apiculate for c. 2 mm, apiculum brownish; *pistillate zone* 3–4 mm long × c. 1.5 mm in diam., with 3

or 4 spirals of pistils; *pistils* rhombic-globose, c. 0.5 mm in diam., lime-green; *stigma* sessile, umbonate, c. ½ diameter of ovary, papillate at anthesis; *pistillodes* 1–3 at base of pistillate zone, squat fusiform, sub-equalling pistils, white; *interstice* with c. 2 rows of *scale-like staminodes*, these c. 1.5 mm long × c. 2 mm wide, wedge-shaped, with thicker edge distal, white, initially erect, then spreading, later (post-anthesis) becoming green and persisting to cover developing fruit; *staminate zone* 3–4 mm long × c. 3.5 mm in diam., consisting of 3 or 4 rows of flowers; *staminate flowers* creamy white; *stamen* c. 1.3 mm across; *filament* strap-shaped, short; *connective* prismatic; *thecae* inserted ventrally, ellipsoid, c. 1 mm long × c. 0.5 mm wide, smooth; *thecae horns* very short, c. 0.3 mm long, setaceous, directed outward; *appendix* bluntly cylindrical, 5–7 mm long × 3.5–4 mm in diam., cream; *appendix staminodes* obpyramidal, irregularly polygonal, lowermost c. 1 mm in diam., individually differentiated, with a slight ventral suture, upper staminodes smaller, c. 0.5 mm in diam., often somewhat coalesced, all tops slightly echinate, with larger staminodes also with a raised echinate rim. *Fruiting spathe* funnel-form, c. 1 cm in diam., with shield-shaped staminodes persistent, turning pale green, spent distal part of spadix falling; *Fruit* and *seed* not seen.

Ecology — *Bucephalandra oblangceolata* is rheophytic on riverside shales under moist to wet lowland forest below 100 m above sea level.

Distribution — Bahagian Miri and Limbang (Sarawak) and in Brunei.

Remarks — *Bucephalandra oblangceolata* is the only *Bucephalandra* species recorded for Brunei, where it occasionally co-occurs with *Aridarum caulescens* M. Hotta (e.g. at Sungai Belalong). In Mulu National Park (Sarawak), *B. oblangceolata* occurs sympatrically on shales with *A. purseglovei* (Furtado) M. Hotta, and allopatrically with *B. muluensis*, the latter restricted to Mulu's karst limestone.

Commercial names — None.

Additional specimens seen — BRUNEI DARUSSALAM: Brunei-Muara: Lumapas, Kampung Lumapas, Bukit Sa'eh, c. 04°51'N, 114°55'E, 15 Jun 1995, *Ariffin Kalat & al BRUN 16768* (BRUN!, K!, SAR!); Bukit Lumapas, base of Bukit Saeh, c. 04°51'N, 114°55'E, 12 Oct 1994, *P. C. Bygrave 45* (BRUN!, K!, L!); Lumapas, Kampung Lumapas, Bukit Sa'eh, 3 May 1994, *Joffre Hj. Ali Ahmad BRUN 15395* (BRUN!). Temburong: Sungai Belalong, 21 Jun 1989, *K. M. Wong WKM 1179* (BRUN!, SAR!). — MALAYSIAN BORNEO: SARAWAK: Bahagian Miri: Marudi, Long Lama, Mulu National Park, Long Langsat, Sungai Langsat, draining into Sungai Tutoh, 04°00'03.5"N, 114°48'49.8"E, 9 Aug 2006, *P. C. Boyce & al. AR-1989* (SAR!, SBC!); Long Lama District, Camp 1,

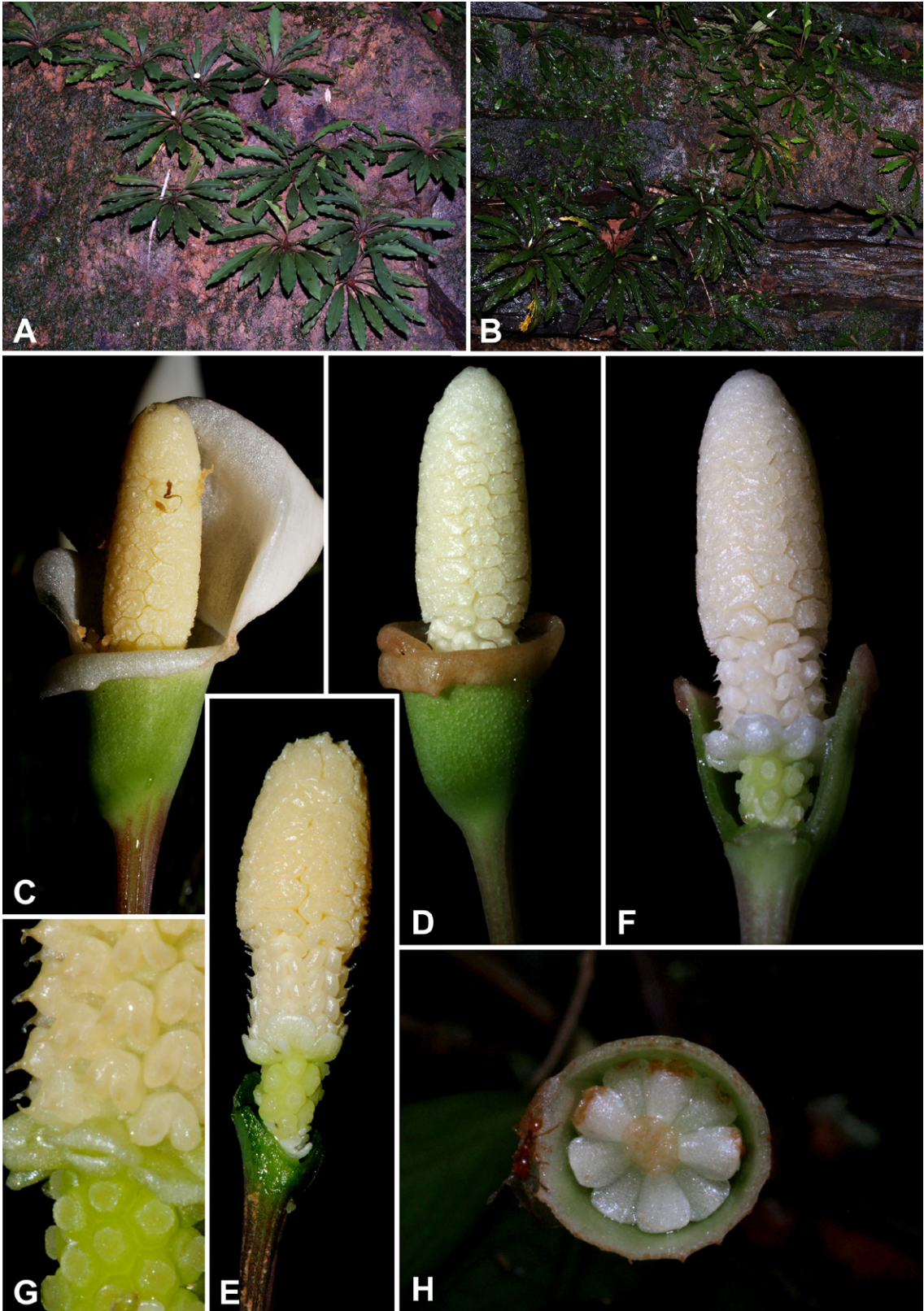


Fig. 15. *Bucephalandra oblanceolata* – A & B: plants in habitat; C: inflorescence at staminate anthesis; D: inflorescence at staminate anthesis, spathe limb shed to leave a deliquesced collar; E: spadix at staminate anthesis, spathe artificially removed; note that interstice staminodes and staminate flower thecae are erect; F: spadix at staminate anthesis, spathe limb fallen naturally, nearside of lower spathe artificially removed; note reflexed interstice staminodes and reflexed thecae; G: detail of staminate flowers and interstice staminodes; H: infructescence during early development with interstice staminodes sealing entrance to persistent lower spathe. – Photographs: A, D, F & H from P. C. Boyce & al. AR-2277; B & C from P. C. Boyce & al. AR-2247; E from P. C. Boyce & al. AR-2310; G from P. C. Boyce & al. AR-1989; all by P. C. Boyce.

S of camp, 12 Feb 1978, *C. Hansen 304 sub Royal Geographical Society's Mulu Expedition 1977–1978* (C!, K!, SAR!). Bahagian Limbang: Nanga Medamit, Mulu N.P., Sungai Empangau, tributary from Sungai Mendalam, 04°13'41.6"N, 114°52'50.5"E, 30 Sep 2007, *P. C. Boyce & al. AR-2247* (SAR!, SBC!); Nanga Medamit, Mulu N.P., Sungai Tamang, tributary from Sungai Mendalam, 04°13'20.9"N, 114°53'08.0"E, 2 Oct 2007, *P. C. Boyce & al. AR-2277* (SAR!, SBC!, SING!); Nanga Medamit, Mulu N.P., Melinau gorge, 3 Oct 2007, *P. C. Boyce & al. AR-2310* (SAR!, SBC!).

20. *Bucephalandra oncophora* S. Y. Wong & P. C. Boyce, **sp. nov.** – Fig. 16 & 24D.

Holotype: Indonesian Borneo, Kalimantan Barat, Kabupaten Sekadau, Kecamatan Nanga Taman, nickel mine, 22 May 2012, *K. Nakamoto AR-3932* (BO!; isotypes: SAR!, SBC!, SING!).

Diagnosis — *Bucephalandra oncophora* is one of two species (the other is *B. vespula*) in which the staminodes of the lower appendix are rounded and conspicuously larger than the upper staminodes. *B. oncophora* differs from *B. vespula* by the stipitate (not sessile) stigmas, and by the lower appendix staminodes irregularly rounded with a conspicuous ventral suture, with the lower $\frac{1}{4}$ – $\frac{1}{3}$ of the appendix conspicuously wider than the rest of the appendix. *B. oncophora* also differs from *B. vespula* by the much longer (c. 1.5 mm vs c. 3 mm) arcuate cylindrical pistillodes at the base of the pistillate flower zone.

Description — Small obligate rheophytic herbs to 14 cm tall. *Stem* erect, in older plants creeping and rooting with active portion sub-erect. *Leaves* to c. 8 together, spreading; *petiole* 3.5–4 cm long \times c. 2 mm in diam., adaxially canaliculate, scabrid, reddish, sheathing at extreme base, wings extended into a very narrowly triangular ligular portion to 1.5 cm long; *blade* elliptic, 9–11 cm long \times 2.5–3 cm wide, coriaceous, semi-glossy dark green adaxially, paler yellowish reddish green abaxially, base cuneate, apex rounded and apiculate for c. 5 mm, margin undulate; *midrib* abaxially and adaxially prominent, strongly reddish abaxially; *primary lateral veins* 3 or 4 on each side, diverging at c. 35° and running to a marginal vein; *interprimary veins* finer; *secondary venation* adaxially \pm obscure, abaxially faint; *tertiary venation* adaxially obscure, forming a faint tessellate reticulum. *Inflorescence* solitary; *peduncle* exceeding petioles, 8–12 cm long \times 3 mm in diam., longitudinally sulcate, medium green with ridges dark red. *Spathe* oblong-ovate, not constricted, 6–7.5 cm long; *lower spathe* narrowly funnel-form, green, persistent; *limb* gaping, then caducous, creamy white, apiculate for c. 4 mm, apiculum green. *Spadix* 4–4.5 cm long; *pistillate zone* 4–7 mm long \times 3–4 mm in diam., with 3 or 4 spirals of pistils; *pistils* polygonal-globose, often radially 3- or

4-sulcate, c. 0.5 mm in diam., lime-green; *stigma* stipitate, capitate, c. $\frac{1}{2}$ diameter of ovary, producing a large stigmatic droplet at pistillate anthesis; *pistillodes* 2–4 at base of pistillate zone, arcuate cylindrical and much-exceeding pistils, c. 3 mm long, cream; *interstice* with c. 2 rows of *scale-like staminodes*, these c. 2 mm long \times c. 2.3 mm wide, margins recurved, initially erect, then spreading, initially white, later (post-anthesis) becoming green and persisting to cover developing fruit; *staminate zone* 1–1.5 mm long \times 5–7 mm in diam., weakly conic, consisting of 6 or 7 rows of flowers; *staminate flowers* greenish; *stamen* comparatively large, c. 1 mm across; *filament* short, stout; *connective* inverted spatulate; *thecae* inserted ventrally, globose-ellipsoid, c. 1 mm long \times c. 0.5 mm wide, smooth; *thecae horns* very short, c. 0.2 mm long, spreading; *appendix* bluntly cylindrical, somewhat constricted $\frac{1}{4}$ – $\frac{1}{3}$ from base with area below constriction noticeably wider than remainder of appendix, 2–2.5 cm long \times 5–7 mm in diam., greenish cream; *appendix staminodes* dimorphic, those of basal $\frac{1}{4}$ – $\frac{1}{3}$ of spadix rounded and umbonate, with a ventral suture (resembling inflated staminate flowers), c. 2 mm in diam., those of remainder of spadix irregularly polygonal, truncate or nearly so, lower few with a suture, remainder not, 0.5–1 mm in diam. *Infructescence* not known.

Ecology — *Bucephalandra oncophora* is rheophytic on nickel-bearing Pentlandite along streams under perhumid lowland forest at c. 60 m above sea level.

Distribution — Known only from the type locality.

Etymology — Latinized from Greek, *onkos* (bulk, mass or tumour) and *phoros* (bearing), hence tumour-bearing, in allusion to the diagnostic staminodes on the lower part of the appendix.

Remarks — *Bucephalandra oncophora* is closely similar to *B. vespula*, which occurs some 45 km to the NE on sandstone riverside rocks.

Commercial names — None.

21. *Bucephalandra pubes* S. Y. Wong & P. C. Boyce, **sp. nov.** – Fig. 17 & 24E.

Holotype: Indonesian Borneo, Kalimantan Barat, Kabupaten Sekadau, Kecamatan Sekadau, 3 Feb 2012, *K. Nakamoto AR-3760* (BO!; isotypes: SAR!, SBC!, SING!).

Diagnosis — *Bucephalandra pubes* is uniquely diagnosed in the genus by the pubescent staminate flowers.

Description — Small obligate rheophytic herbs to 12 cm tall. *Stem* erect, in older plants creeping and rooting with active portion sub-erect. *Leaves* many together, erect;

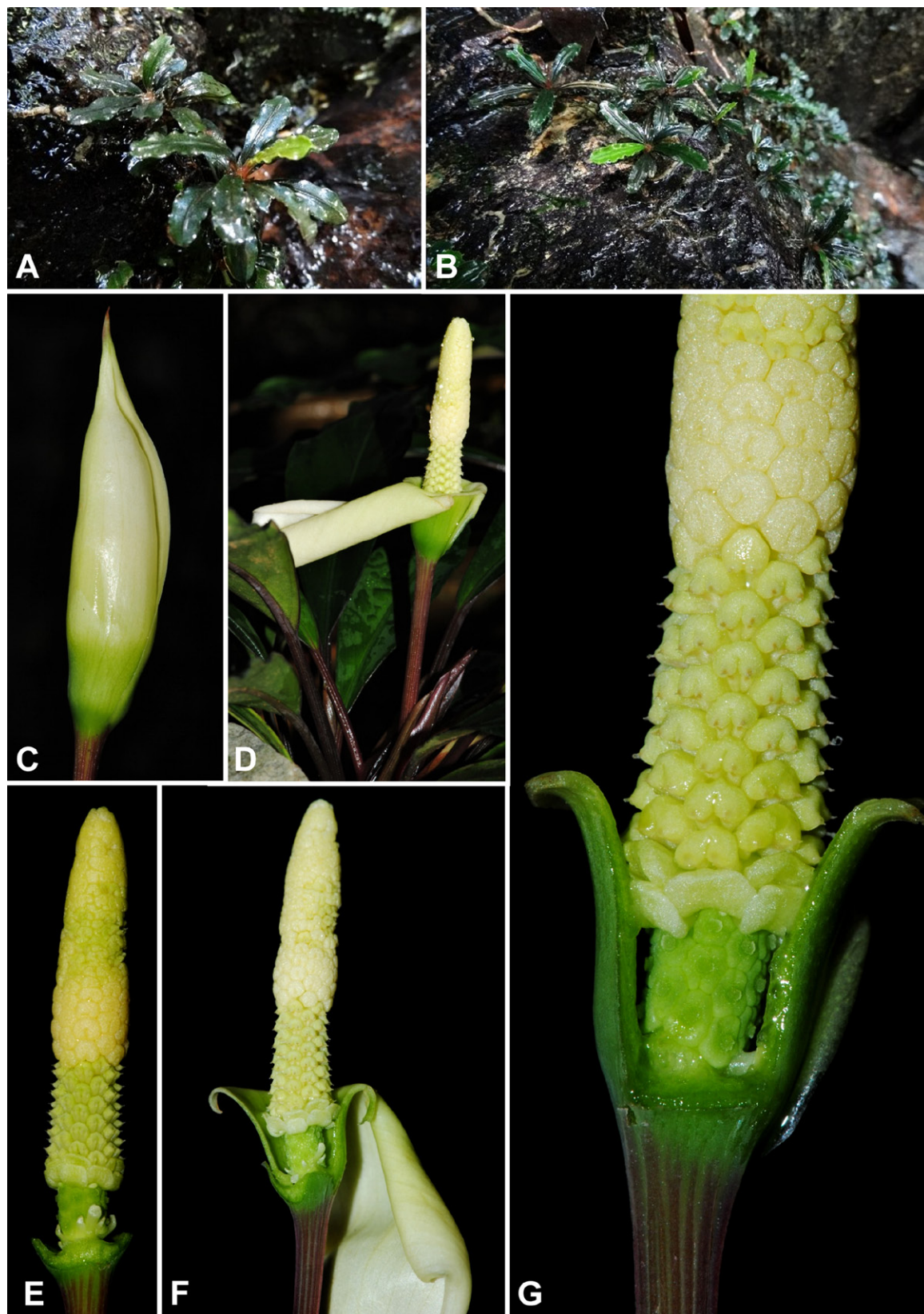


Fig. 16. *Bucephalandra oncophora* – A & B: plants in habitat; C: inflorescence at pistillate anthesis; D: inflorescence at staminate anthesis, spathe limb shedding; E: spadix at pistillate anthesis, spathe artificially removed; note different form of distal and proximal appendix staminodes; F: spadix at staminate anthesis, spathe limb fallen naturally, nearside of lower spathe artificially removed; note interstice staminodes are beginning to reflex; compare posture of thecae horns with those in E; G: detail of staminate flowers and reflexed interstice staminodes, nearside lower spathe artificially removed. – Photographs: from K. Nakamoto AR-3932; A & B by K. Nakamoto; C–G by P. C. Boyce.

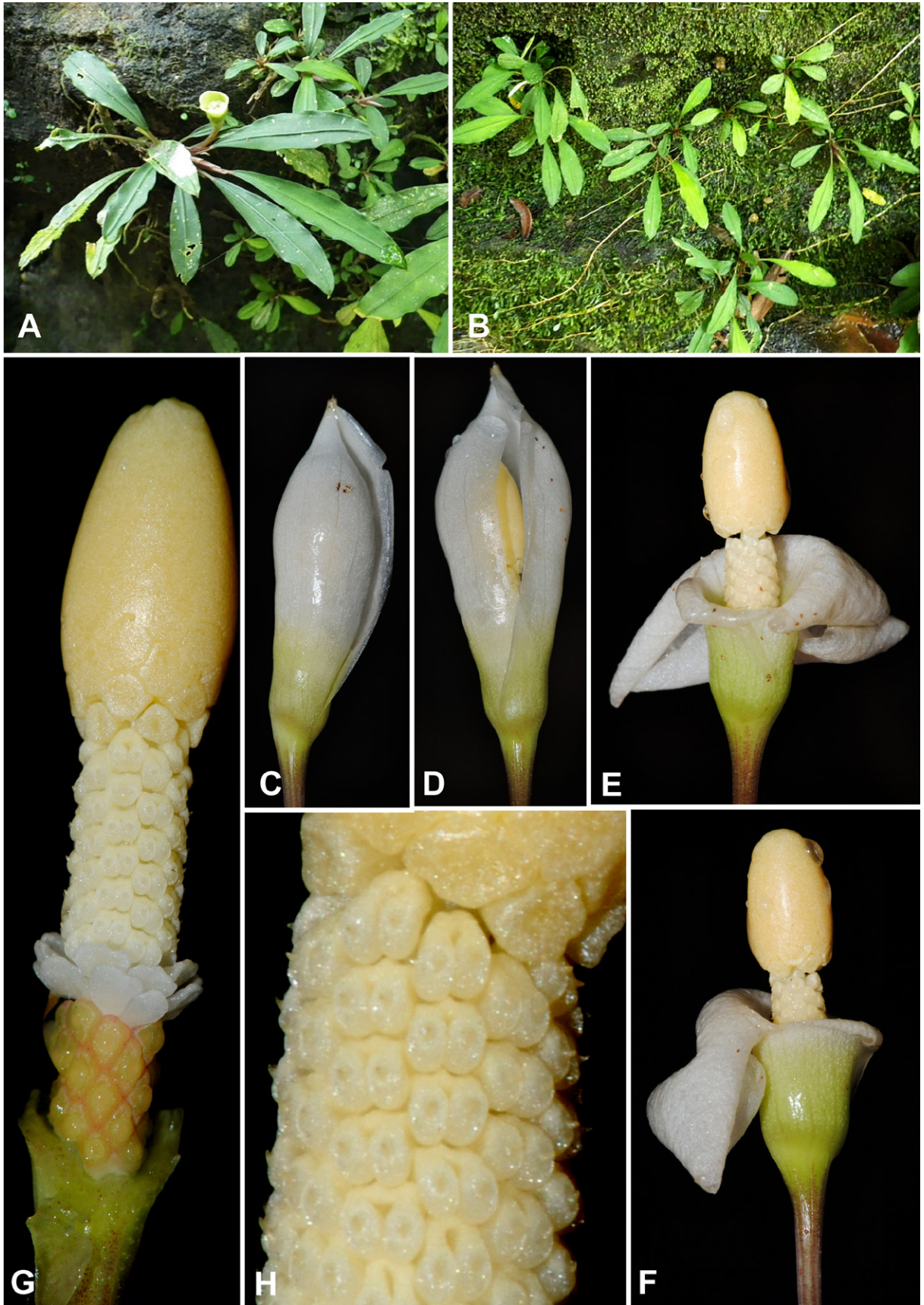


Fig. 17. *Bucephalandra pubes* – A & B: plants in habitat; C & D: inflorescence at pistillate anthesis; E & F: inflorescence at staminate anthesis, spathe limb shedding; G: spadix at pistillate anthesis, spathe artificially removed; H: detail of staminate flowers. – Photographs: from K. Nakamoto AR-3760; A & B by K. Nakamoto; C–H by P. C. Boyce.

petiole 4–5 cm long \times c. 2 mm in diam., adaxially canaliculate, scabrid, reddish, sheathing at extreme base, wings extended into a very narrowly triangular ligular portion to 2 cm long; *blade* narrowly elliptic, 11–12 cm long \times c. 1.5 cm wide, thinly coriaceous, semi-glossy bright green adaxially, paler yellowish whitish green abaxially, base cuneate, apex rounded and apiculate for c. 3 mm, margin somewhat undulate; *midrib* abaxially and adaxially prominent, strongly reddish abaxially; *primary lateral* and *interprimary veins* indistinct; *secondary venation* adaxially \pm obscure, abaxially conspicuously reticulate; *tertiary venation* obscure. *Inflorescence* several together alternating with foliage leaves; *peduncle* equalling petioles, 4–5 cm long, weakly longitudinally sulcate and medium green with copious reddish minute speckles. *Spathe* broadly ovate, 3.5–4 cm long, fusiform in bud with widest part coinciding with spadix appendix, spathe not constricted but with a weak expansion c. $\frac{1}{2}$ way up lower spathe and another weaker at limb junction with lower spathe; *lower spathe* funnel-form, glossy greenish yellow, persistent; *limb* gaping to form a wide distal slit at pistillate anthesis, then at staminate anthesis reflexing with tip and margins recurving, then caducous, white, apiculate for c. 2 mm, apiculum green. *Spadix* 2–3.5 cm long; *pistillate zone* 5–6 mm long \times c. 1.5 mm in diam., with 3 or 4 spirals of pistils; *pistils* rhombic-globose, c. 0.5 mm in diam., pale cream prior to anthesis, edges of ovary turning pink at pistillate anthesis; *stigma* sessile, capitate, c. $\frac{1}{2}$ diameter of ovary, producing a large stigmatic droplet at pistillate anthesis; *pistillodes* 2 or 3 at base of pistillate zone, tongue-shaped, c. 0.3 mm long, glossy white; *interstice* with 2 rows of *scale-like staminodes*, these c. 1.5 mm long \times c. 1 mm wide, wedge-shaped, initially erect, then spreading, initially white, later (post-anthesis) becoming green and persisting to cover developing fruits; *staminate zone* slender cylindrical, 7–11 mm long \times c. 3 mm in diam., consisting of 6–9 rows of flowers; *staminate flowers* pubescent, cream; *stamen* comparatively large, c. 1 mm across; *filament* short, stout; *connective* very slender strap-shaped, pubescent; *thecae* inserted ventrally at tip (appearing to hang from filament), cylindrical, c. 1 mm long \times c. 0.5 mm wide, pubescent; *thecae horns* very short, c. 0.25 mm long, upward-turned; *appendix* ellipsoid, 1–1.5 cm long \times 5–7 mm in diam., cream; *appendix staminodes* fused and individually indistinguishable except for lowermost few, these irregularly polygonal, c. 1 mm in diam., surface of appendix smooth and somewhat glossy. *Fruiting spathe* funnel-form, c. 1 cm in diam., pale green, with shield-shaped staminodes persistent, turning green, spent distal part of spadix falling; *berry* depressed globose, 1–1.8 mm long \times 1–1.5 mm in diam.

Ecology — *Bucephalandra pubes* is rheophytic on granite rocks and boulders under lowland moist forest, recorded at less than 100 m above sea level.

Distribution — Known only from the type locality.

Etymology — Latin, *pubes* (downy, especially of reproductive parts), used in allusion to the pubescent staminate flowers.

Remarks — *Bucephalandra pubes* is one of the most readily identifiable species by virtue of the pubescent staminate flowers with very short thecae horns.

Commercial names — None.

22. *Bucephalandra pygmaea* (Becc.) P. C. Boyce & S. Y. Wong in *Webbia* 67: 142. 2012 = *Microcasia pygmaea* Becc. in *Bull. Reale Soc. Tosc. Ort.* 4: 180. 1879; *Engl. in Beccari, Malesia* 1: 290, t. 22, f. 21–24. 1883; *Nat. Pflanzenfam.* 2(3): 132, fig. 85. 1889; *Pflanzenr.* 55 (IV.23Da): 128, fig. 77A–D. 1912. – Fig. 24F. *Holotype*: Malaysian Borneo, Sarawak, Bahagian Sarikei, Julau, Sungai Entabai, 28 Oct 1867 (annotated on FI sheet), or Sep 1867 (annotated on B sheet, and stated in Beccari 1879), or 26 Oct 1867 (stated in Beccari 1902, 1904), *O. Beccari PB* 3883 (FI-B!; isotype: B!).

Description — See Boyce & Wong (2012: 142–144).

Ecology — *Bucephalandra pygmaea* is an obligate rheophyte on shale, or very occasionally sandstone, along streams and waterfalls under moist or perhumid lowland forest at between 10–55 m above sea level.

Distribution — Malaysian Borneo (Sarawak), in Sarikei and Kapit and Indonesian Borneo, in Kapuas Hilir and Kapuas Hulu. Scattered, but often forming significant populations.

Etymology — Latin, *pygmaeus* (from Greek, *pygmaios*, dwarf), in allusion to the stature of the whole plant.

Remarks — The taxonomic history of *Bucephalandra pygmaea* was detailed by Boyce & Wong (2012).

Commercial names — None accurately applied.

23. *Bucephalandra sordidula* S. Y. Wong & P. C. Boyce, *sp. nov.* – Fig. 18 & 24G.

Holotype: Indonesian Borneo, Kalimantan Barat, Kabupaten Melawi, Kecamatan Nanga Pinoh, 33 km S of Nanga Pinoh and 11 km before Kotabaru junction of logging road to Kalimantan Tengah, 00°40'21.6"S, 111°44'03.4"E, 16 Oct 2012, *K. Nakamoto AR-4042* (BO!; isotypes: SAR!, SBC!, SING!).

Diagnosis — *Bucephalandra sordidula* is overall most similar to *B. pygmaea* but is readily differentiated by the

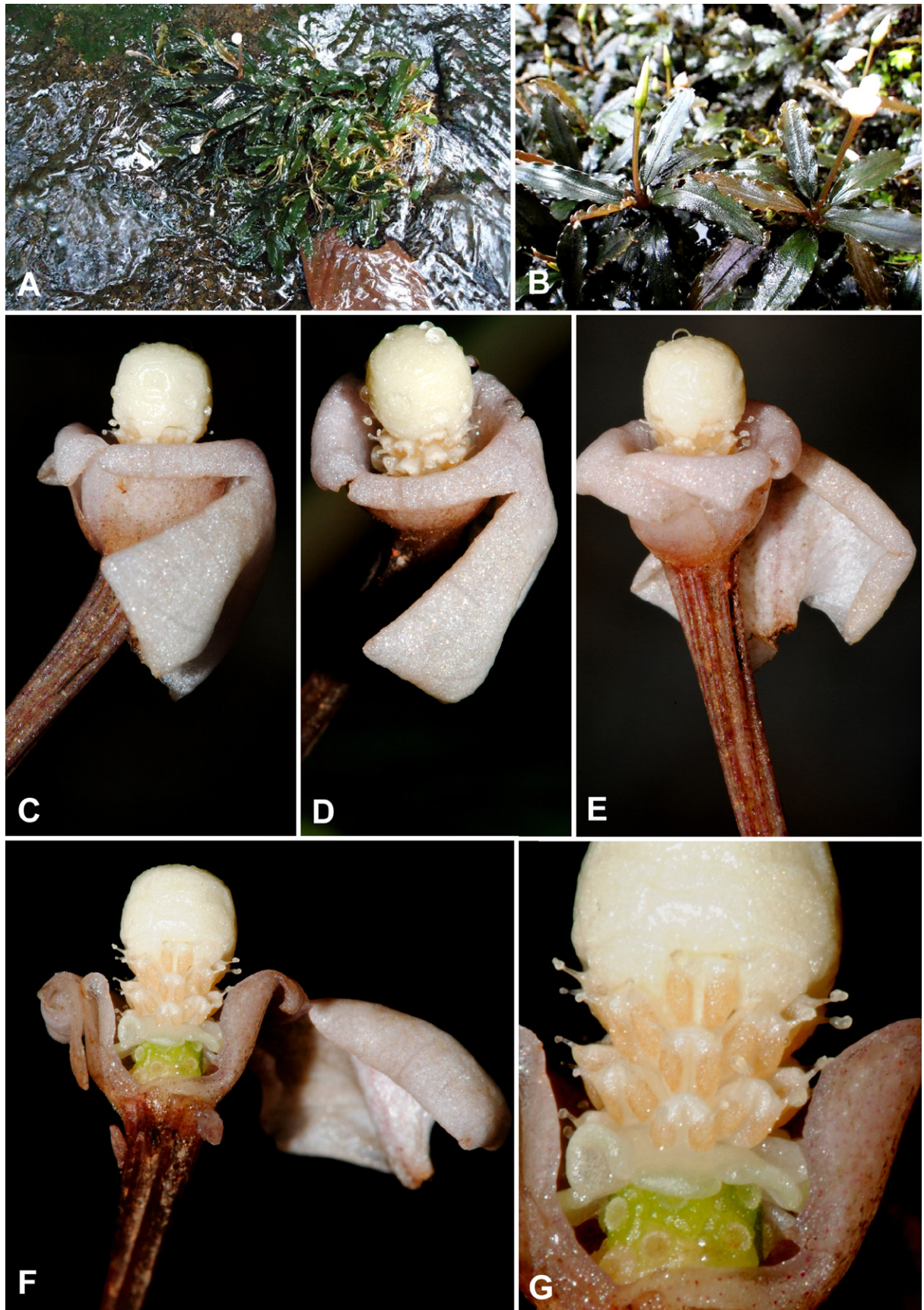


Fig. 18. *Bucephalandra sordidula* – A & B: plants in habitat; C–G: inflorescence at staminate anthesis; note droplets visible on tips of thecae horns; G: spadix, nearside of spathe limb artificially removed; note also droplets on thecae horn tips and reflexed interstice staminodes. – Photographs: from *M. Lo AR-4042*; A & B by M. Lo; C–G by P. C. Boyce.

proportionately very long peduncle, globose appendix, reddish brown (not white) thecae of the staminate flowers, and by the lower spathe broadly salver-form at anthesis with the exterior stained pinkish brown. *Bucephalandra sordidula* is reminiscent of *B. diabolica*, although the latter is readily identified by the thecae horns at least as long as the rest of the staminate flower. The much-elongated peduncle is shared with *B. catherineae*, from which *B. sordidula* differs by the broadly spatulate (not linear) undulate (not strongly crispulate) leaf blades.

Description — Diminutive obligate rheophytic herbs c. 2.5 cm tall, occurring in extensive patches. *Stem* creeping with active portion sub erect, branching repeatedly, stems c. 1–2.5 mm in diam. *Leaves* appressed to ground, scattered along stems; *petiole* 0.5–1 cm long × c. 2 mm in diam., adaxially canaliculate, greenish brown, sheathing at extreme base, wings extended into a very narrowly triangular ligular portion to 1 cm long; *blade* obovate, 3–5 cm long × 1–1.5 cm wide, thinly coriaceous, olive-green adaxially, paler and reddish abaxially, base cuneate to sub-decurrent, apex rounded and apiculate for c. 1 mm, margin undulate to crispulate; *midrib* adaxially somewhat prominent, abaxially much finer, although reddish and therefore conspicuous; *primary lateral* and *interprimary veins* very fine and not differentiated, c. 8 veins per side; *secondary venation* abaxially forming a fine reticulum. *Inflorescence* solitary; *peduncle* greatly exceeding petioles, 5.5–7 cm long, conspicuously longitudinally sulcate, dark reddish brown with deeper brown speckles. *Spathe* broadly ovate, not constricted, c. 1.5 cm long; *lower spathe* funnel-form, dirty white with reddish brown speckles, especially in lower ½, later turning green with brownish speckles, persistent; *limb* gaping to form a distal slit at pistillate anthesis, reflexing at staminate anthesis, then caducous, externally dirty white with variable amounts of brownish red speckles, interior dirty white, apiculate for c. 1 mm, apiculum reddish brown. *Spadix* 6–7.5 mm long; *pistillate zone* c. 2 mm long × c. 1.5 mm in diam., with c. 2 spirals of pistils; *pistils* rhombic-globose, c. 0.3 mm in diam., bright green; *stigma* sessile, umbonate, c. ½ diameter of ovary, papillate at anthesis; *pistillodes* absent; *interstice* with 2 incomplete rows of *scale-like staminodes*, these c. 0.5 mm long × c. 0.7 mm wide, weakly spatulate, glossy white, later (post-anthesis) becoming green and persisting to cover developing fruit; *staminate zone* c. 1.5 mm long × c. 2 mm in diam., consisting of 2 or 3 rows of flowers; *staminate flowers* somewhat pinkish; *stamen* c. 1 mm across; *filament* short, stout; *connective* strap-shaped, glossy white; *thecae* inserted ventrally, ellipsoid, c. 1 mm long × c. 0.3 mm wide, smooth, pinkish, speckled darker pink; *thecae horns* c. ½ length of associated theca, setaceous, upward-pointing; *appendix* globose, c. 3 mm long × c. 2 mm in diam., glossy waxy white; *appendix staminodes* obpyramidal, somewhat regularly polygonal (individual staminodes not easily distinguished), flat-topped,

c. 1 mm in diam. *Fruiting spathe* widely funnel-form, c. 5 mm in diam., with shield-shaped staminodes persistent, turning green, spent distal part of spadix falling; *fruits* and *seeds* not seen.

Ecology — *Bucephalandra sordidula* occurs on Upper Cretaceous granite rocks along rivers under perhumid lower hill forest at c. 200 m above sea level.

Distribution — Known only from the type locality.

Etymology — From Latin, *sordidus* (dirty) and the diminutive suffix *-ula*, hence *sordidula*, the little dirty one, in reference to the brownish pink staining on the spathe exterior.

Remarks — *Bucephalandra sordidula* is one of the most distinctive species of the taxonomically troublesome *Bucephalandra* Pygmaea Complex by virtue of the remarkably long peduncles and the salver-form lower spathe. *Bucephalandra sordidula* is also one of the few species (the other is *B. belindae*) to flower with the plants fully submerged, the long peduncles raising the spathe and spadix above the water.

Commercial names — ‘Titan’.

24. *Bucephalandra tetana* S. Y. Wong & P. C. Boyce, **sp. nov.** – Fig. 19 & 24H.

Holotype: Indonesian Borneo, Kalimantan Barat, Kabupaten Sintang, Kecamatan Serawai, Gunung Alat, N of Nanga Serawai and 120 km E of Nanga Pinoh, 00°04'09.0"S, 112°25'38.6"E, 17 May 2013, K. Nakamoto AR-4146 (BO!; isotypes: SAR!, SBC!, SING!).

Diagnosis — *Bucephalandra tetana* is immediately recognizable by the very stiff leaf blades, which are adaxially punctate. The slightly brain-like spadix appendix is somewhat reminiscent of that of *B. muluensis*, but the glossy (not matte) interstice pistillodes are diagnostic.

Description — Diminutive obligate rheophytic herbs c. 3 cm tall, forming patches up to 25 cm across. *Stem* creeping and rooting with active portion semi-erect, branching repeatedly, branches 0.5–3 cm long × 1.5–2 mm in diam., usually bright reddish. *Leaves* many together, densely arranged along stems, mostly semi-erect, sometimes appressed to substrate; *petiole* c. 1 cm long × c. 2 mm in diam., adaxially canaliculate, reddish, sheathing at extreme base, wings extended into a very narrowly triangular ligular portion to 1 cm long; *blade* obovate to elliptic, 4–5 cm long × c. 2 cm wide, very stiffly coriaceous, semi-glossy dark green with minute whitish punctulations adaxially, paler yellow-reddish to reddish, less often green abaxially, and supplied with numerous minute reddish punctulations, base cuneate,

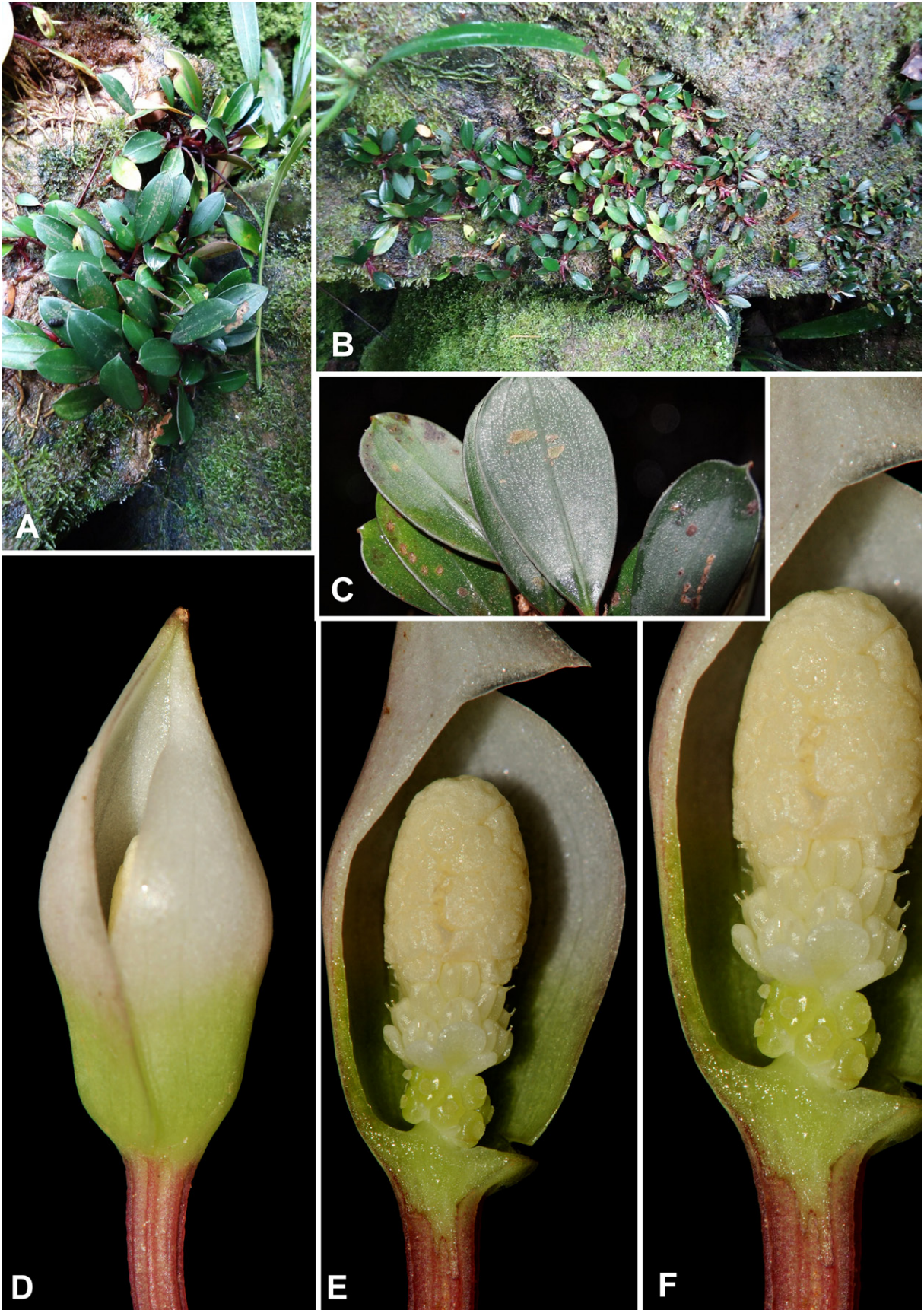


Fig. 19. *Bucephalandra tetana* – A & B: plants in habitat; C: detail of leaf blades; note stiff texture and punctulate adaxial surface; D: inflorescence at pistillate anthesis; E: spadix, nearside of spathe limb artificially removed; F: detail of spadix. – Photographs: from K. Nakamoto AR-4146; A–C by K. Nakamoto; D–F by P. C. Boyce.

apex rounded and stiffly apiculate for c. 3 mm, margin somewhat recurved; *midrib* abaxially and adaxially very prominent, reddish abaxially; *primary lateral veins* 3 on each side, diverging at c. 60° and running to a marginal vein; *interprimary veins* alternating with primaries, slightly finer; all other venation obscure. *Inflorescence* solitary; *peduncle* exceeding petioles, 2–3 cm long, conspicuously longitudinally sulcate, reddish, colour intensifying along ridges. *Spathe* broadly ovate, not constricted, c. 2 cm long; *lower spathe* funnel-form, pale bright green, persistent; *limb* gaping at pistillate anthesis, opening via a wide slit as far at lower spathe, then caducous, white with a faint pink flush, apiculate for c. 2 mm, apiculum deep reddish brown. *Spadix* c. 1 cm long; *pistillate zone* c. 1.5 mm long × c. 1.5 mm in diam., with 2 or 3 incomplete spirals of pistils; *pistils* rhombic-globose, c. 0.5 mm in diam., lime-green; *stigma* sessile, umbonate, slightly impressed, c. ½ diameter of ovary, papillate at anthesis; *pistillodes* absent; *interstice* with 1 row of *scale-like staminodes*, these c. 1 mm long × c. 1.2 mm wide, margin somewhat thickened, glossy white; *staminate zone* c. 2.5 mm long × c. 2.5 mm in diam., consisting of 2 or 3 rather irregular rows of flowers; *staminate flowers* ascending, creamy white; *stamen* c. 1 mm across; *filament* short, slender; *connective* strap-shaped; *thecae* inserted ventrally, ellipsoid, c. 1 mm long × c. 0.5 mm wide, smooth; *thecae horns* c. ¼ length of associated theca, setaceous, spreading; *appendix* bluntly ellipsoid, c. 5 mm long × 2.5–3 mm in diam., cream; *appendix staminodes* well-defined, columnar, regularly polygonal, truncate, c. 1 mm in diam., upper surface somewhat brain-like. *Infructescence* not seen.

Ecology — *Bucephalandra tetana* is rheophytic on exposed but mossy basalt river rocks under perhumid upper hill to lower montane forest at c. 900 m above sea level.

Distribution — Known only from the type locality.

Etymology — From Latin adjective, *tetanus* (from Greek, *tetanos*, stiff, rigid), in reference to the leaf blades.

Remarks — *Bucephalandra tetana* is another member of the diverse *Bucephalandra* Pygmaea complex. It is easily distinguished by the rigid leaf blades, which are unique for the genus and seem to be an adaptation to the exposed habitat that the species favours.

Commercial names — ‘Penelope’.

25. *Bucephalandra ultramafica* S. Y. Wong & P. C. Boyce, **sp. nov.** – Fig. 20 & 24I.

Holotype: Malaysian Borneo, Sabah, Sandakan, Kinabatangan, Telupit, Gunung Tawai, 05°35'45.6"N, 117°04'36.7"E, 18 Dec 2012, *M. Lo* AR-4094 (SAN!; isotypes: SAR!, SBC!, SING!).

Diagnosis — *Bucephalandra ultramafica* is unique by the combination of deeply ridged petioles, narrow deep green glossy leaves, and a bullet-shaped appendix. The leaf blades are somewhat reminiscent of those of *B. goliath*, but *B. ultramafica* never develops the long pendent stems diagnostic of *B. goliath*, and the spadix appendix and appendix staminodes are of quite different form.

Description — Small obligate rheophytic herbs to c. 16 cm tall, occurring as individuals or small clumps. *Stem* creeping with active portion semi-erect, c. 1.5 cm in diam. *Leaves* several together, erect to spreading; *petiole* 2–4 cm long × c. 2 mm in diam., adaxially canaliculate, strongly longitudinally ridged, deep red, sheathing at extreme base, wings extended into a very narrowly triangular ligular portion to 2.4 cm long; *blade* oblanceolate to narrowly elliptic, 8–12 cm long × 1–1.5 cm wide, rather thickly coriaceous, semi-glossy very dark green adaxially, pale olive-green with very numerous minute purple glands abaxially, base cuneate, apex acute and apiculate for c. 1.5 mm, margin slightly recurved, *midrib* abaxially and adaxially very prominent, reddish abaxially; *primary lateral veins* c. 5 on each side, diverging at c. 45° and running to a marginal vein; *interprimary veins* ± invisible; *secondary venation* ± obscure. *Inflorescence* solitary; *peduncle* exceeding petioles, 4–6 cm long, very conspicuously longitudinally sulcate, distal-most part with scattered minute verrucae, deep red. *Spathe* broadly ovate, not constricted, 2–3 cm long; *lower spathe* funnel-form, green with many red speckles and red lines that are extensions of peduncle ridges, persistent; *limb* inflating at anthesis, gaping distally at pistillate anthesis to create a slit-like aperture, then reflexing at staminate anthesis, finally caducous, externally white with plentiful minute red speckles and a red median line, internally white, apiculate for c. 2 mm, apiculum reddish brown. *Spadix* 2–2.5 cm long; *pistillate zone* 3–4 mm long × c. 2.5 mm in diam., with c. 3 spirals of pistils; *pistils* rhombic to compressed globose, c. 0.5 mm in diam., lime-green; *stigma* sessile, umbonate, c. ½ diameter of ovary, papillate and secreting a conspicuous stigmatic droplet at pistillate anthesis; *pistillodes* 2–5 at base of pistillate zone, clavate, c. 0.25 mm tall, glossy white; *interstice* with 3 rows of *scale-like staminodes*, these c. 1.8 mm long × c. 2 mm wide, glossy white; *staminate zone* 4–5 mm long × 5–6 mm in diam., consisting of 3 or 4 rows of flowers; *staminate flowers* white; *stamen* c. 1.5 mm across; *filament* short, block-like; *connective* tongue-shaped; *thecae* inserted ventrally, ellipsoid, c. 1 mm long × c. 0.5 mm wide, smooth; *thecae horns* c. ⅓ length of associated theca, setaceous, upward-pointing; *appendix* conoid to bullet-shaped, 5–8 mm long × 5–7 mm in diam., cream; *appendix staminodes* columnar, tops polygonal with very rounded angles, somewhat umbonate with a small central depression, c. 0.5–1 mm in diam., cream. *Fruiting spathe* funnel-form, c. 1 cm in diam., yellow-green on a red peduncle, with shield-shaped staminodes persistent, turning

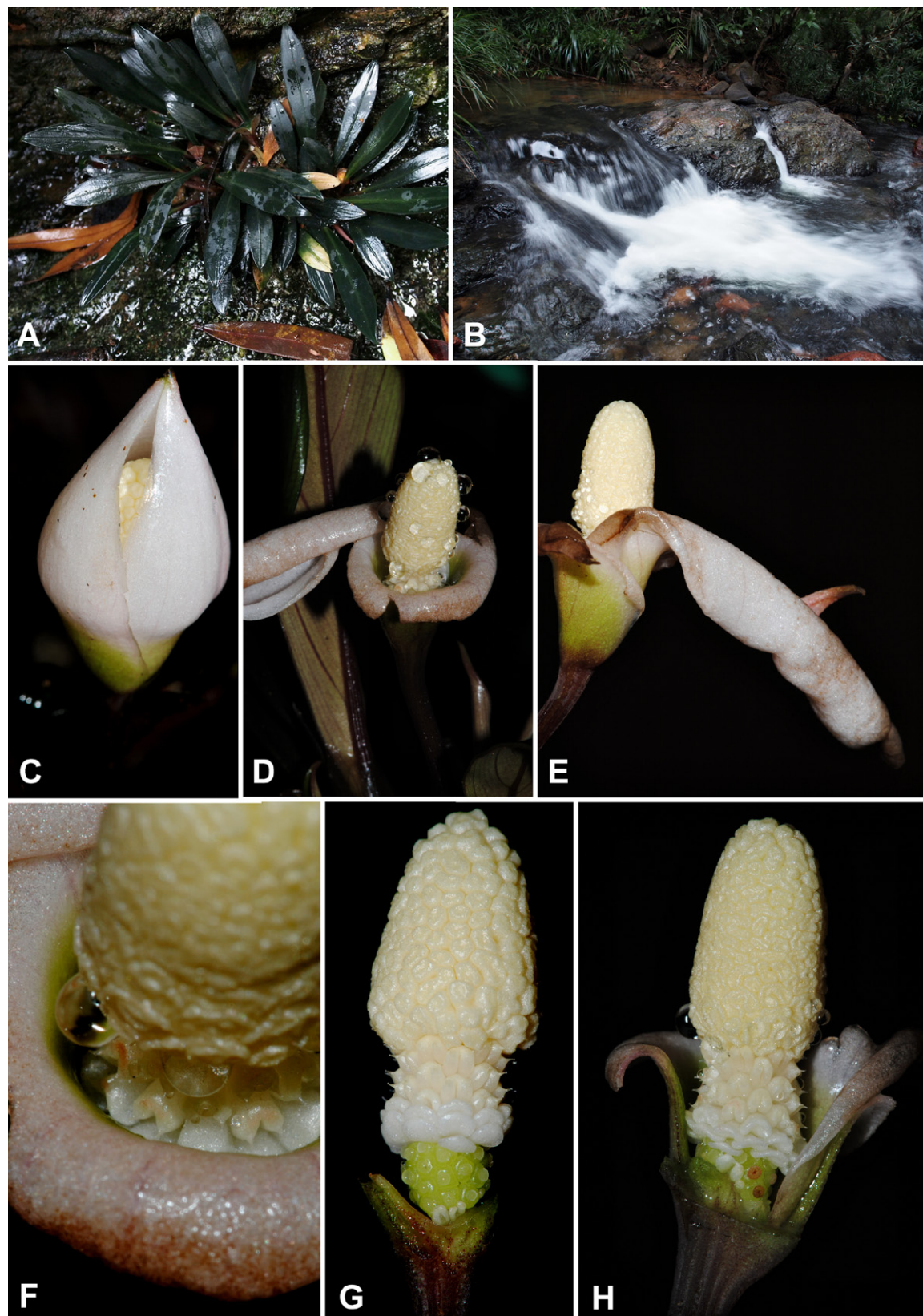


Fig. 20. *Bucephalandra ultramafica* – A: plants in habitat; B: habitat; *B. ultramafica* occurs on bare rocks in flow of water; C: inflorescence at pistillate anthesis; D & E: inflorescence at staminate anthesis, spathe limb beginning to shed; note shiny brownish discolouration of spathe limb; F: detail of reflexed interstice staminodes closing entrance to lower spathe; G: spadix at pistillate anthesis, spathe artificially removed; note erect interstice staminodes and staminate flower thecae; H: spadix at staminate anthesis, spathe limb shed naturally, nearside of lower spathe artificially removed. – Photographs: from *M. Lo AR-4094*; A & B by M. Lo; C–H by P. C. Boyce.

yellow green, and spent distal part of spadix falling; *fruits* and *seeds* not seen.

Ecology — *Bucephalandra ultramafica* is restricted to ultramafic (ultrabasic) riverside rocks under lowland moist forest at c. 130 m above sea level.

Distribution — Known only from the type locality.

Etymology — The specific epithet is coined from the obligate geological habitat this species, ultramafic rocks.

Remarks — *Bucephalandra ultramafica* is one of at least two ultramafic-obligate *Bucephalandra* species occurring in Sabah. The second author encountered what is certainly a second undescribed ultramafic-obligate *Bucephalandra* species while undertaking fieldwork at Bidu-Bidu Forest Reserve, Sandakan, Sabah in 2003. A single flowering plant was encountered but circumstances prevented preparation of adequate herbarium material, excepting an immature spadix preserved in alcohol. Recollection at Bidu-Bidu is necessary.

Commercial names — None.

26. *Bucephalandra vespula* S. Y. Wong & P. C. Boyce, **sp. nov.** – Fig. 21 & 24J.

Holotype: Indonesian Borneo, Kalimantan Barat, Kabupaten Sekadau, Kecamatan Sekadau Hilir, Kayu Lapis, S of Kayu Lapis, 00°47'21.3"S, 113°55'15.7"E, 20 Sep 2011, K. Nakamoto AR-3664 (BO!; isotypes: SAR!, SBC!, SING!).

Diagnosis — *Bucephalandra vespula* is one of two species (the other is *B. oncophora*) in which the staminodes of the lower appendix are rounded and conspicuously larger than the upper staminodes. *Bucephalandra vespula* differs from *B. oncophora* by the appendix staminodes being regularly rounded, the zone not conspicuously wider than the rest of the appendix, and each staminode having a conspicuous shallow suture. *Bucephalandra vespula* also differs from *B. oncophora* by the much shorter (1.5 mm vs c. 3 mm) spatulate pistillodes at the base of the pistillate flower zone.

Description — Small obligate rheophytic herbs to 16 cm tall. *Stem* erect, in older plants creeping and rooting with active portion sub-erect. *Leaves* to c. 8 together, spreading; *petiole* 6–8 cm long × c. 2 mm in diam., adaxially canaliculate, scabrid, red, sheathing at extreme base, wings extended into a very narrowly triangular ligular portion to 3 cm long; *blade* elliptic to oblong lanceolate, 9–10.5 cm long × c. 2 cm wide, slightly coriaceous, semi-glossy dark green adaxially, paler yellowish green abaxially, base cuneate, apex rounded and apiculate for c. 5 mm, margin undulate; *midrib* abaxially and adaxially

prominent, strongly reddish abaxially; *primary lateral veins* c. 4 on each side, diverging at c. 55° and running to a marginal vein; *interprimary veins* finer; *secondary venation* adaxially ± obscure, abaxially faint; *tertiary venation* adaxially obscure, forming a faint tessellate reticulum. *Inflorescence* solitary; *peduncle* exceeding petioles, 7–13 cm long × c. 2 mm in diam., longitudinally sulcate, medium green with ridges dark, often somewhat winged near junction with spathe. *Spathe* oblong-ovate, not constricted, 4–5 cm long; *lower spathe* narrowly funnel-form, green, persistent; *limb* gaping to form a longitudinal slit at pistillate anthesis, opening almost flat and tearing from persistent lower spathe at staminate anthesis, then tearing into irregular strips and pieces before falling, then caducous, ivory, apiculate for c. 4 mm, apiculum green. *Spadix* 3–4 cm long; *pistillate zone* 4–7 mm long × 3–4 mm in diam., with 3 or 4 spirals of pistils; *pistils* polygonal-globose, c. 0.5 mm in diam., lime-green; *stigma* stipitate, capitate, c. ½ diameter of ovary, producing a large stigmatic droplet at staminate anthesis; *pistillodes* 2–4 at base of pistillate zone, spatulate, equalling pistils, c. 1.5 mm long, cream; *interstice* with c. 2 rows of *scale-like staminodes*, these c. 2 mm long × c. 2.3 mm wide, margins recurved, initially erect, then spreading, green; *staminate zone* 7–10 mm long × 4–7 mm in diam., weakly conic, consisting of 4 or 5 rows of flowers; *staminate flowers* rather distant, greenish; *stamen* comparatively large, c. 1 mm across; *filament* short, stout; *connective* arching, strap-like, tip thickened, pale green; *thecae* inserted ventrally, globose-ellipsoid, c. 1 mm long × c. 0.4 mm wide, smooth; *thecae horns* very short, c. 0.2 mm, spreading; *appendix* bluntly cylindrical, somewhat constricted ¼–⅓ from base, 2–2.5 cm × 5–7 mm in diam., greenish cream; *appendix staminodes* dimorphic, those of basal ¼–⅓ of spadix rounded polygonal, 2–2.5 mm in diam., with a central tiny hole, those of remainder of spadix irregularly polygonal, truncate or nearly so, 0.5–1 mm in diam. *Fruiting spathe* funnel-form, c. 1.5 cm in diam.; *fruits* and *seeds* not seen.

Ecology — *Bucephalandra vespula* occurs on shaded granite rocks bordering and in swift-flowing streams under moist lowland forest at c. 100 m above sea level.

Distribution — So far only known from the type locality.

Etymology — From Latin, *vespa* (wasp) and the diminutive suffix *-ula*, hence *vespula*, a small wasp. This is an allusion to the plan-view shape of the individual staminate flowers, which resembles the head of a wasp.

Remarks — *Bucephalandra vespula* shares with *B. oncophora* having the staminodes of the lower appendix morphologically dissimilar to those of the upper appendix.

Commercial names — None.

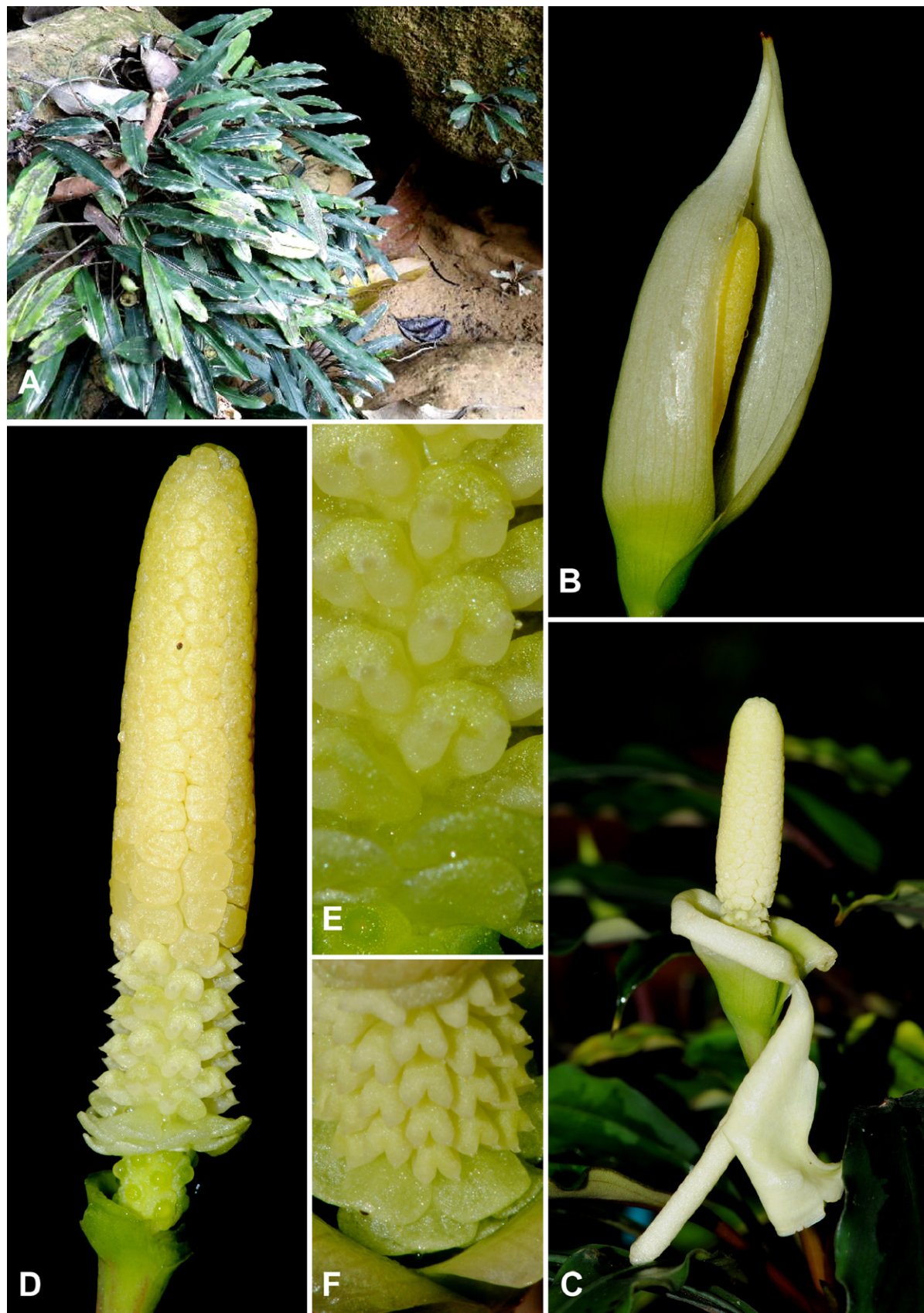


Fig. 21. *Bucephalandra vespula* – A: plants in habitat; B: inflorescence at pistillate anthesis; C: inflorescence at staminate anthesis, spathe limb beginning to shed; D: spadix at staminate anthesis, spathe artificially removed; note reflexed interstice staminodes and staminate flower thecae; E & F: detail of staminate (E) and pistillate (F) anthesis. – Photographs: from K. Nakamoto AR-3664; A by K. Nakamoto; B–F by P. C. Boyce.

27. *Bucephalandra yengiae* P. C. Boyce, **sp. nov.** – Fig. 22 & 24K.

Holotype: Indonesian Borneo, Kalimantan Timur, Kabupaten Kutai Kartanegara, Kecamatan Tabang, 00°34'33.2"N, 116°01'05.9"E, 17 Oct 2012, K. Nakamoto AR-4050 (BO!; isotypes: SAR!, SBC!, SING!).

Diagnosis — *Bucephalandra yengiae* is distinguished from all other species of *Bucephalandra* by having erect thecae horns at staminate anthesis, with the thecae fully exposed, and echinate appendix staminodes.

Description — Small obligate rheophytic herbs to c. 10 cm tall. *Stem* creeping with active portion sub-erect, c. 4 mm in diam. *Leaves* up to 13 together; *petiole* 3–4 cm long × c. 1.5 mm in diam., adaxially narrowly canaliculate, red-brown, sheathing at extreme base, wings extended into a very narrowly triangular ligular portion to 2 cm long; *blade* ovate to broadly elliptic, 7–9.5 cm long × 3–4.5 cm wide, rather softly coriaceous, glossy medium green adaxially, paler yellowish greenish red abaxially, base broadly cuneate, apex acute and apiculate for c. 1.5 mm, margin usually straight; *midrib* abaxially and adaxially prominent, reddish abaxially; *primary lateral veins* c. 4 on each side, diverging at c. 45° and running to a marginal vein; *interprimary veins* almost invisible; *secondary venation* adaxially ± obscure. *Inflorescence* solitary; *peduncle* exceeding petioles, 5–9 cm long, conspicuously longitudinally sulcate, reddish stained. *Spathe* elliptic ovate, not constricted, c. 3 cm long; *lower spathe* funnel-form, yellow-green, shading to red at peduncle insertion, persistent; *limb* inflating at pistillate anthesis, then gaping to produce a slit approximately at junction of limb and lower spathe, caducous at staminate anthesis, white, acuminate, and apiculate for c. 4 mm, apiculum green. *Spadix* c. 1.5 cm long; *pistillate zone* cylindrical, c. 5 mm long × c. 3 mm in diam., with c. 4 spirals of pistils; *pistils* rhombic-globose, c. 0.5 mm in diam., pale green; *stigma* sessile, polygonal umbonate, c. ½ diameter of ovary, papillate at anthesis, pinkish; *pistillodes* 1 or 2 at base of pistillate zone, squat fusiform, subequalling pistil, white; *interstice* with 1 row of *scale-like staminodes*, these c. 1.5 mm long × c. 2 mm wide, margins reflexed, initially erect, then spreading, white, later (post-anthesis) becoming green and persisting to cover developing fruit; *staminate zone* c. 3 mm long × c. 3 mm in diam., consisting of c. 3 rows of flowers; *staminate flowers* ascending, cream; *stamen* c. 1 mm across × c. 1.5 mm long; *filament* short, slender; *connective* slender strap-shaped; *thecae* inserted ventrally, completely obscuring filament, ellipsoid, c. 1 mm long × c. 0.5 mm wide, smooth; *thecae horns* c. ½ length of associated theca, setaceous, upward-directed; *appendix* cylindrical, c. 6 mm long × c. 4 mm in diam., cream; *appendix staminodes* columnar, irregularly pentagonal or polygonal, 0.3–0.5 mm in diam., tops echinate, glossy. *Fruiting spathe* funnel-form, c. 1 cm in diam., with shield-shaped staminodes persistent, turning green, spent distal part of spadix falling; *fruits* and *seeds* not seen.

Ecology — *Bucephalandra yengiae* occurs on vertical water-splashed Jurassic-Cretaceous deepwater sedimentary rocks beneath perhumid to moist lowland forest at c. 50 m above sea level.

Distribution — Known only from the type locality.

Eponymy — Named for the first author, whose phylogenetic work is bringing about much-improved understanding, and consequently considerable taxonomic change, in terrestrial and rheophytic Asian aroids.

Remarks — The echinate spadix appendix makes *Bucephalandra yengiae* a highly distinctive species not easily mistaken for any other described species of *Bucephalandra*. Sterile plants, with impressed primary veins of the adaxial surface of the leaf blades, are highly reminiscent of juvenile plants of *Ooia*.

Commercial names — None.

Key to the species of *Bucephalandra*

1. Staminodes of appendix mostly individually well-defined, polygonal 2
 - Staminodes of appendix usually individually ill-defined, often coalescent; if individual staminodes discernible then plan view never rhomboidal 13
2. Appendix staminodes verrucate or brain-like ... 3
 - Appendix staminodes smooth 6
3. Staminate flowers hastate with a distinct basal claw (viewed from above), entire stamen flexing downward from base at staminate anthesis; dorsal surface of connective flat, margins verrucate; thecae separated by a deep sinus, thecae horns stout, spreading, deep orange-brown. Kalimantan Barat: Gunung Tajam, granite 10. *Bucephalandra forcipula*
 - Staminate flowers globose, sessile, thecae flexing outward at anthesis; dorsal surface of connective rounded, smooth; thecae appressed, not separated by a distinct sinus, thecae horns very slender, straight, white ... 4
4. Appendix bullet-shaped to conoid, accounting for c. ½ of spadix. Sarawak: Sri Aman, sandstones ...
 - 9. *Bucephalandra elliptica*
 - Appendix ellipsoid, accounting for c. ⅔ of spadix . 5
5. Leaf blades thinly leathery, bright green, not punctate; interstice staminodes matte white. Sarawak: Mulu National Park, lowland limestone
 - 18. *Bucephalandra muluensis*
 - Leaf blades very stiff, deep bluish green and adaxially punctate; interstice staminodes glossy white. Kalimantan Barat: Gunung Alat, basalt above 900 m . . .
 - 24. *Bucephalandra tetana*
6. Staminate flowers arching upward from spadix; thecae dark orange, embedded in connective and presented on exposed ventral surface of stamen at staminate an-

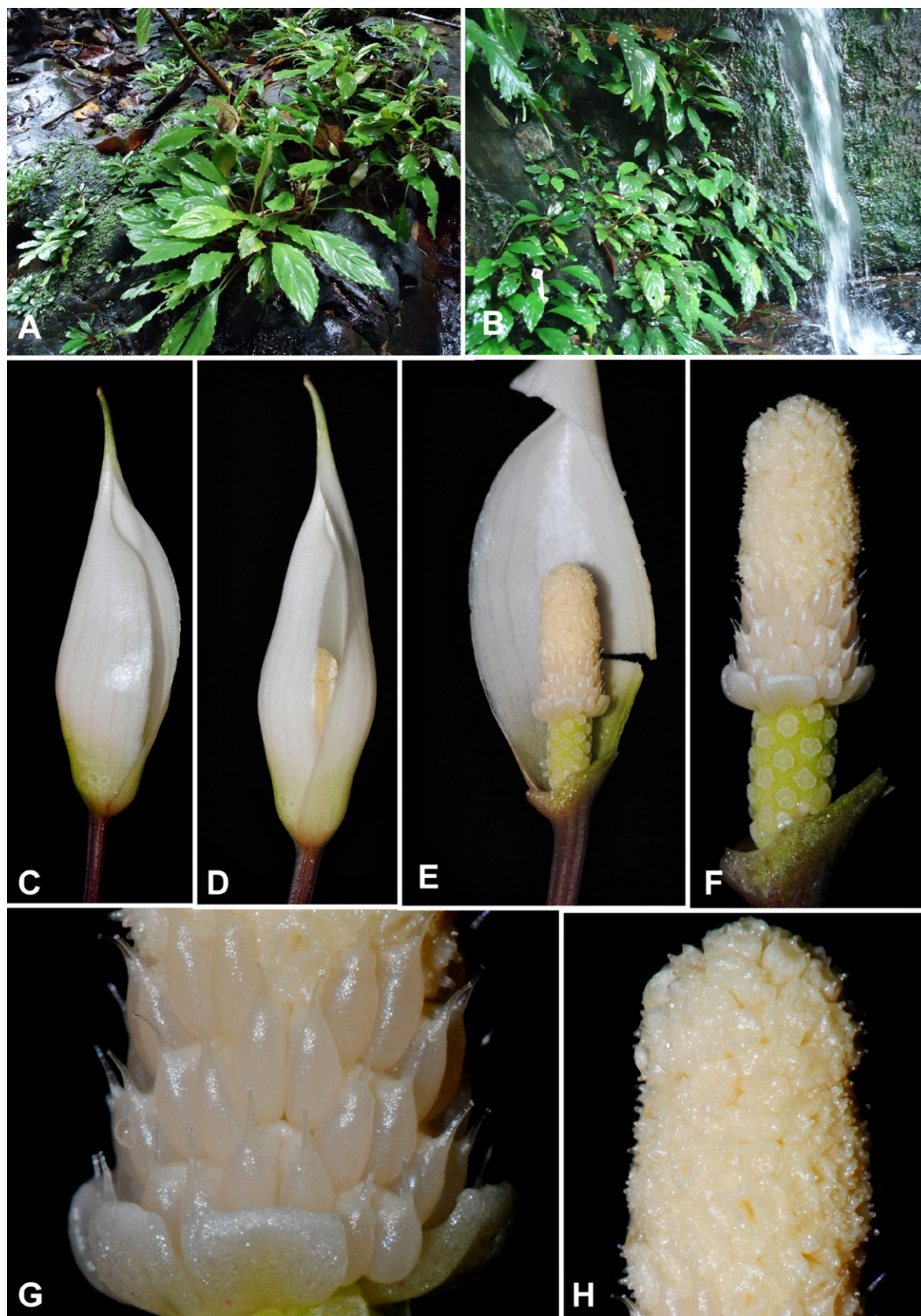


Fig. 22. *Bucephalandra yengiae* – A & B: plants in habitat; C & D: inflorescence at pistillate anthesis; E: inflorescence at onset of staminate anthesis, nearside part of spathe artificially removed; split in spathe limb is natural and marks beginning of shedding process; F: spadix at onset of staminate anthesis, spathe artificially removed; note reflexing interstice staminodes and staminate flower thecae; G: detail of staminate flowers and interstice staminodes; H: detail of appendix. – Photographs: from K. Nakamoto AR-4050; A & B by K. Nakamoto; C–H by P. C. Boyce.

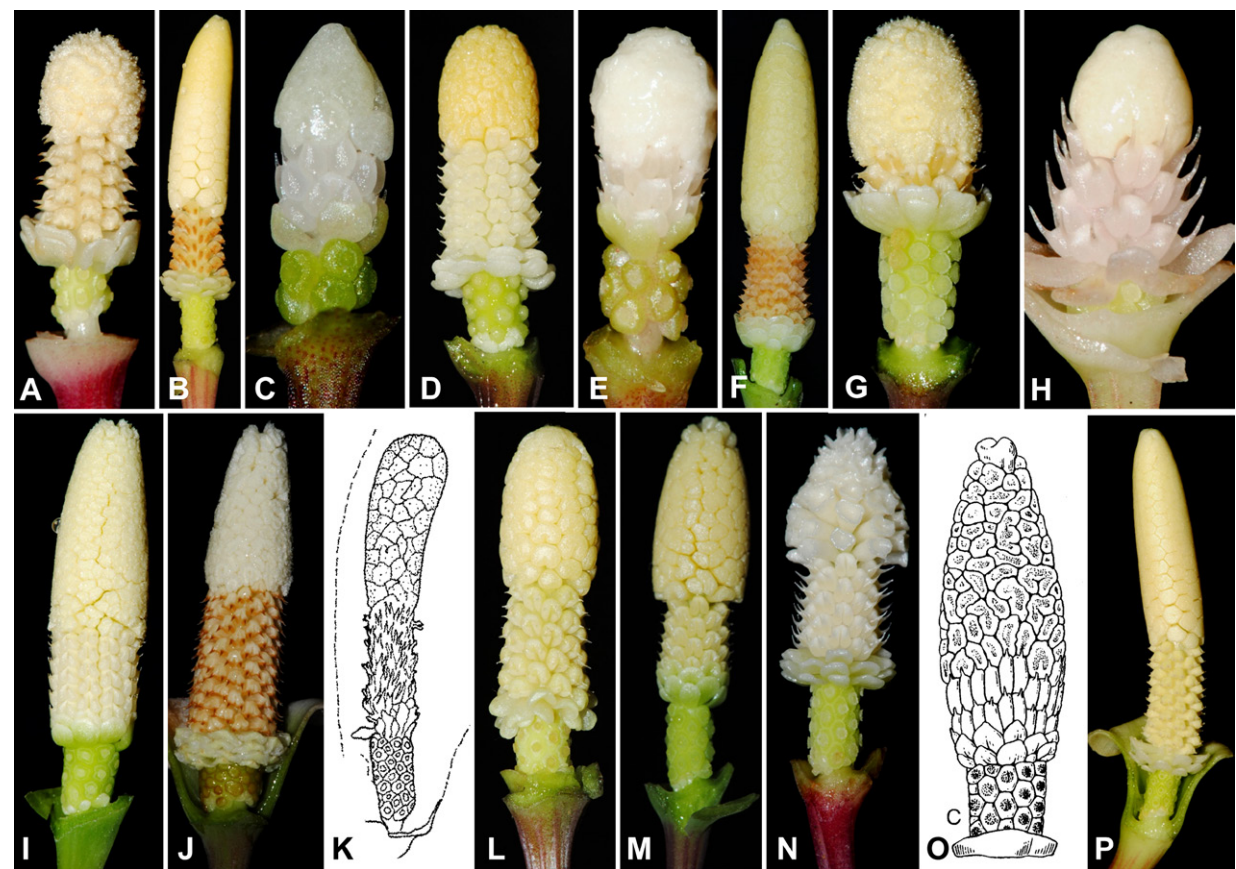


Fig. 23. Spadix comparisons of fresh and drawn spadices (spathe artificially removed) of *Bucephalandra* – A: *B. akantha* from K. Nakamoto AR-3884; B: *B. aurantiithea* from K. Nakamoto AR-3937; C: *B. belindae* from K. Nakamoto AR-3754; D: *B. bogneri* from P. C. Boyce & al. AR-94; E: *B. catherinae* from K. Nakamoto AR-3903; F: *B. chimaera* from K. Nakamoto AR-3846; G: *B. chrysokoupa* from K. Nakamoto AR-3977; H: *B. diabolica* from M. Lo AR-4027; I: *B. elliptica* from K. Nakamoto AR-3564; J: *B. forcipula* from K. Nakamoto AR-3772; K: *B. gigantea* reproduced from Bogner (1984: 160, fig. 2); L: *B. goliath* from K. Nakamoto AR-3848; M: *B. kerangas* from P. C. Boyce & S. Y. Wong AR-2595; N: *B. kishii* from K. Nakamoto AR-4005; O: *B. magnifolia* reproduced from Okada & Mori (2000: 3, fig. 2C); P: *B. minotaur* from K. Nakamoto AR-3951. – Photographs: by P. C. Boyce.

thesis; thecae horns very short, directed downward. Kalimantan Barat: Sekadau and Nanga Taman, granite **2. *Bucephalandra aurantiithea***

– Staminate flowers with filament and connective perpendicular to spadix; thecae not embedded in connective, presented on dorsal surface of stamen at staminate anthesis; thecae horns directed upward **7**

7. Appendix fusiform or bullet-shaped, base wider than staminate flower zone **8**

– Appendix weakly conoid, weakly clavate, or ellipsoid, base equalling staminate flower zone; staminate flowers cream **9**

8. Appendix fusiform, base tapering; staminate flowers orange. Kalimantan Barat: Nanga Taman, granite ..
..... **6. *Bucephalandra chimaera***

– Appendix bullet-shaped, base truncate; staminate flowers cream, thecae inflated. SW Sarawak/Kalimantan Barat: Klingkang Range, kerangas
..... **13. *Bucephalandra kerangas***

9. Staminate flowers with thecae horns equalling thecae in length; interstice staminodes with minutely serrate tips; petiole 15–28 cm long, leaf blade 18–25 cm

long × 6–7 cm wide, with 16–20 closely spaced primary lateral veins on each side
..... **11. *Bucephalandra gigantea***

– Staminate flowers with thecae horns much shorter than thecae in length; interstice staminodes with smooth tips; leaves not as above **10**

10. Sinus between thecae extending up front of staminate flower; plants with long stout stems mainly rooting at base with remainder free and pendent; leaf blades glossy dark green. Kalimantan Barat: Nanga Taman and Nanga Pinoh, granite
..... **12. *Bucephalandra goliath***

– Sinus between thecae not (or only barely) extending to front of staminate flower; plants tufted, stem slender, rooting along its entire length; leaf blades matte olive-green **11**

11. Staminodes of lower ⅓ of appendix flat and morphologically identical to those of upper appendix. Kalimantan Barat: Sekadau/Melawi Regencies boundary, granite **16. *Bucephalandra minotaur***

– Staminodes of lower appendix irregularly rounded, larger than upper appendix staminodes **12**

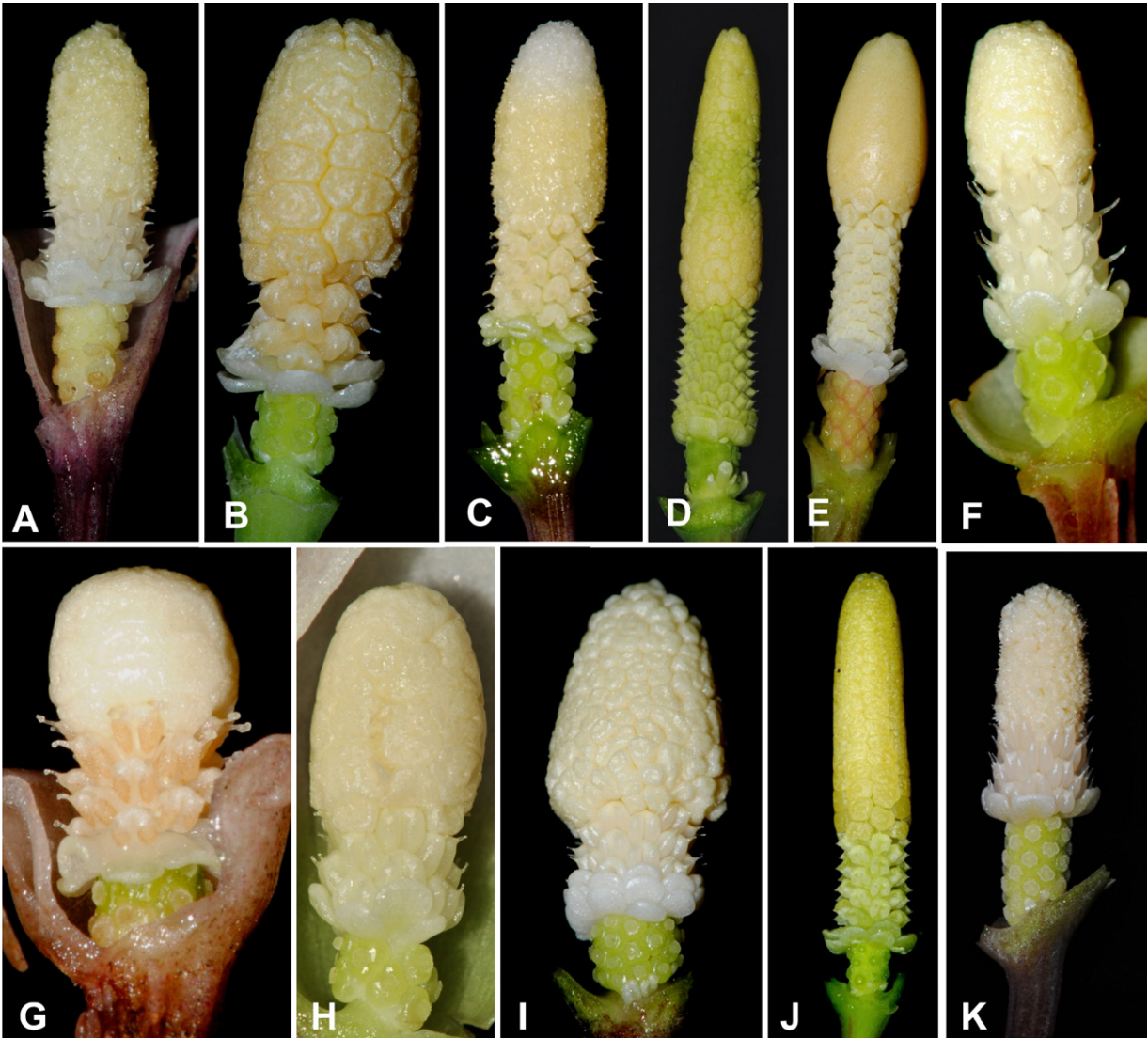


Fig. 24. Spadix comparisons of fresh spadices (spathe artificially removed) of *Bucephalandra* – A: *B. sp. nov. aff. motleyana* from K. Nakamoto AR-4051; B: *B. muluensis* from P. C. Boyce & al. AR-3937; C: *B. oblanceolata* from P. C. Boyce & al. AR-1989; D: *B. oncophora* from K. Nakamoto AR-3932; E: *B. pubes* from K. Nakamoto AR-3760; F: *B. pygmaea* from P. C. Boyce & S. Y. Wong AR-3632; G: *B. sordidula* from M. Lo AR-4042; H: *B. tetana* from K. nakamoto AR-4146; I: *B. ultramafica* from M. Lo AR-4094; J: *B. vespula* from K. Nakamoto AR-3664; K: *B. yengiae* from K. Nakamoto AR-4050. – Photographs: by P. C. Boyce.

12. Stigmas sessile; lower appendix staminodes regularly rounded, not conspicuously wider than rest of appendix, each staminode with a conspicuous shallow suture. Kalimantan Barat: Kayu Lapis, sandstone . . .
..... **26. *Bucephalandra vespula***

– Stigmas stipitate; lower appendix staminodes irregularly rounded, conspicuously wider than rest of appendix, each staminode without a suture. Kalimantan Barat: Nanga Taman, Pentlandite . . .
..... **20. *Bucephalandra oncophora***

13. Appendix staminodes smooth **14**

– Appendix staminodes papillate or brain-like . . . **19**

14. Staminate flowers pubescent; spadix appendix ellipsoid; staminate flower zone slender cylindrical, narrower than appendix. Kalimantan Barat: Kabupaten Sekadau, granite **21. *Bucephalandra pubes***
- Staminate flowers glabrous; spadix appendix globose or conic or ellipsoid, equalling or narrower than staminate flower zone **15**

15. Leaf blades narrowly linear, usually with strongly crispulate margins **16**

– Leaf blades various, but never linear, margins flat to undulate but never crispulate **17**

16. Stems much-branched and elongated, not rooting along their length except occasionally; spadix appendix conic, comprised of very few, large staminodes, glassy. Kalimantan Barat: Nanga Pinoh, granite cascades under permanent water flow
..... **3. *Bucephalandra belindae***

– Stems little-branched, creeping, rooting profusely to rocks; spadix appendix globose, comprised of several small staminodes, waxy white. Kalimantan Utara:

- Gunung Sungai Pendan, rheophytic on basalt
 **5. *Bucephalandra catherineae***
17. Thecae horns very long, at least as long as rest of staminate flower. Kalimantan Barat: Bukit Baka, granite **8. *Bucephalandra diabolica***
- Thecae horns short, not exceeding thecae in length **18**
18. Peduncle very long, up to 10 cm, slender; appendix globose; thecae of staminate flowers reddish brown; lower spathe broadly salver-form at anthesis, exterior stained pinkish brown. Kalimantan Barat: Nanga Pinoh, granites **23. *Bucephalandra sordidula***
- Peduncle short, often less than 1 cm, at most 3 cm, stout; appendix ellipsoid; thecae of staminate flowers white; lower spathe obconic at anthesis, exterior white. Sarawak: Kanowit, Song and Rejang river basins, shales **22. *Bucephalandra pygmaea***
19. Appendix staminodes papillate **20**
- Appendix staminodes not papillate **24**
20. Spathe limb deep yellow to medium orange; interstice staminodes with minutely serrate tips. Kalimantan Utara: Long Berang, granite
 **7. *Bucephalandra chrysokoupa***
- Spathe limb white; interstice staminodes not serrate **21**
21. Spadix appendix globose; staminate flowers with thecae divergent, thecae horns stout, straight at staminate anthesis. SW Sarawak and NW Kalimantan, granite and metamorphosed sandstone
 **1. *Bucephalandra akantha***
- Spadix appendix ellipsoid or cylindrical; staminate flowers with thecae parallel, and thecae horns either downward-curved or erect at staminate anthesis **22**
22. Thecae horns erect at staminate anthesis, thecae fully exposed; spadix appendix cylindrical, staminode surface papillae echinate. Kalimantan Timur: Tabang, ancient deepwater sedimentaries
 **27. *Bucephalandra yengiae***
- Thecae horns downward-curved at staminate anthesis, thecae obscured; spadix appendix ellipsoid, staminode epidermis papillate but never echinate **23**
23. Thecae horns with a ring of verrucae at base. Kalimantan Selatan, (?)ultramafics
 **17. *Bucephalandra motleyana***
- Thecae horns without a ring of verrucae at base. NW Sarawak, Brunei, shales
 **19. *Bucephalandra oblanceolata***
24. Appendix staminodes lax, surface often excavated; thecae horns longer than thecae, ascending at staminate anthesis; leaf blades with primary veins prominently raised. Kalimantan Barat: Gunung Saran, granites above 1200 m **14. *Bucephalandra kishii***
- Appendix staminodes densely arranged; thecae horns shorter than thecae, ascending at staminate anthesis; leaf blades with primary veins obscure **25**
25. Appendix staminodes c. 1.5 mm in diam.; appendix expanding abruptly at junction with staminate flower zone; leaf blade abaxially with very numerous minute purple glands. Sabah: Gunung Tawai, ultramafics
 **25. *Bucephalandra ultramafica***
- Appendix staminodes c. 3 × 2 mm; appendix equaling width of staminate flower zone; leaf blade abaxially without glands **26**
26. Appendix staminodes yellow; staminate flowers almost globose, in c. 6 rows; petioles c. 3 cm long, leaf blades c. 5 cm long. Sarawak: Penrissen, Serian area, lowland alkaline geologies (limestone and basalt)
 **4. *Bucephalandra bogneri***
- Appendix staminodes white; staminate flowers oblong, in c. 2 rows; petioles c. 10 cm long, leaf blades c. 12 cm long. Kalimantan Utara: Krayan, sedimentaries, above 980 m **15. *Bucephalandra magnifolia***

The role of the interstice staminodes of *Bucephalandra*

As noted above, *Bucephalandra* species are unique among *Araceae* by the presence of motile scale- or shield-shaped staminodes situated at the interstice of the pistillate and staminate flower zones. It has been speculated that these staminodes play a role in manipulating pollinators during anthesis by controlling access to the pistillate flower zone (Bogner 1980; Bogner & Hay 2000), but conclusive observations have been wanting.

Field observations of seven different *Bucephalandra* species (of which one is figured here for illustrative purposes) has established that pistillate anthesis begins 2–3 hours after dawn, with the spathe inflating to create a slit in the upper part of the spathe limb (Fig. 25B), the papillate stigmatic surface becoming sticky, producing a stigmatic droplet at pistillate anthesis, and production of a weak to rather powerful esteric or fruity odour attracting almost exclusively *Colocasiomyia* (*Diptera: Drosophilidae*), although recently *B. aurantiitheca* has been observed to be pollinated by a single species of *Chrysomelidae* (*Coleoptera*) (Fig. 2B). Pistil receptivity is c. 6 hours, and during this time the interstice staminodes and thecae are erect (Fig. 25C). The spathe limb remains in this “gaping” phase for c. 24 hours, but the interstice staminodes begin to lower by the evening of the same day (Fig. 25D, E). By midnight of the same day the tips of the lowered staminodes are pressed on the inner wall of the lower spathe, effectively sealing the lower spathe chamber (Fig. 25D, E). By this time the stigmas are dry and no longer receptive and the inflorescence is in the transition phase from pistillate to staminate anthesis. At no time do the interstice staminodes retain insects in the lower (pistillate) part of the spathe, and by the time they are sealing the lower spathe no insects are present in or on the inflorescence.

Staminate anthesis begins 2–3 hours after dawn on the second day. The staminate flower thecae reflex (Fig. 25E), and a second floral odour emission attracts a new wave of *Colocasiomyia* flies. Soon after this the spathe limb gape increases, and then very rapidly (less than 5 minutes) the

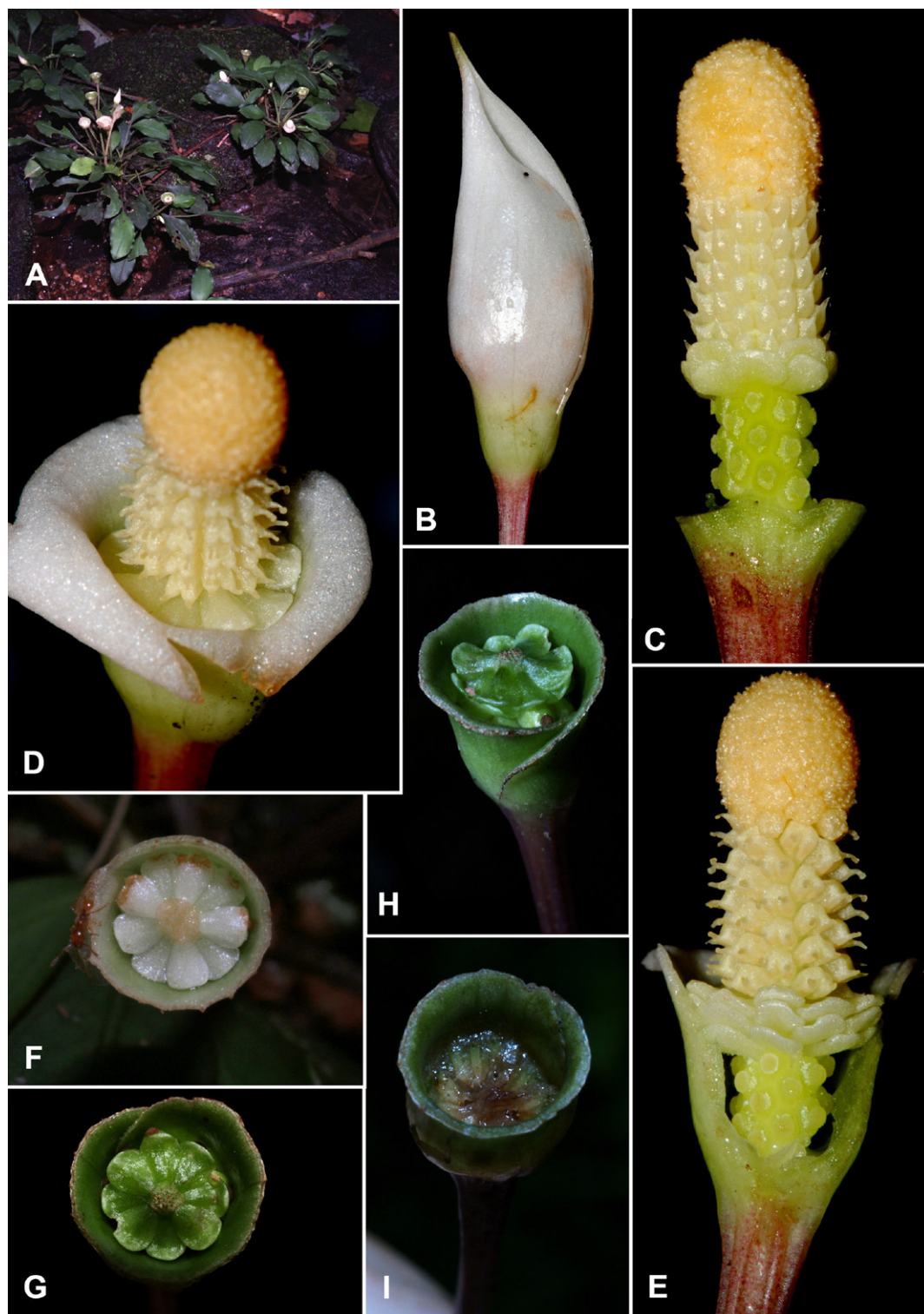


Fig. 25. Functions of interstice staminodes in *Bucephalandra akantha* – A: plants in habitat, inflorescences at various stages of anthesis; B: inflorescence at onset of pistillate anthesis; note inflated spathe with a slit extending from tip to c. $\frac{1}{3}$ length of limb; C: spathe at onset of pistillate anthesis, spathe artificially removed; note erect interstice staminodes and thecae and papillate stigmas; D: inflorescence at staminate anthesis, spathe limb naturally shed; note staminodes sealing entrance to lower spathe and that thecae have reflexed and produced a pollen droplet from tip of horn; E: spathe at staminate anthesis, spathe artificially removed; note reflexed interstice staminodes and thecae, and pollen droplet secreted from tip of thecae horns; F: infructescence c. 1 day after anthesis, spathe limb completely shed, as too are spent parts of spadix; note umbonate scar in middle of still-white interstice staminodes; G: infructescence c. 4 weeks after anthesis; note that staminodes and lower spathe are now green and thickened; tannin cells are just visible on staminodes; H: infructescence c. 7 weeks after anthesis; developing fruits are beginning to push staminodes upward; I: infructescence c. 8 weeks after anthesis; staminodes have been shed and fruits have decomposed to a mucilaginous pulp containing seeds. – Photographs: from P. C. Boyce & S. Y. Wong AR-3889; all by P. C. Boyce.

limb abscises at its junction with the lower spathe (Fig. 25A), with the limb variously splitting and coiling outward from the margin. These rapid spathe limb movements coincide with pollen droplet extrusion from the tips of the thecae horns (Fig. 25D & E). Staminate anthesis lasts c. 1 hour, at the end of which period all pollen droplets have been taken by the flies, and the spathe limb has fallen to leave the funnel-form lower spathe. Dependent on the species, between a few hours and four days after staminate anthesis the spent parts of the spadix above the interstice staminodes are shed to leave a faintly umbonate scar in the middle of a disk of white staminodes (Fig. 25F).

Within a few days of staminate anthesis, and provided fertilization has been successful, the staminodes sealing the persistent lower spathe change from white to green (apparently become photosynthetic), thicken, and harden (Fig. 25G). Most species also have tannin cells visible on the upper surface of the staminode. The staminodes remain in this condition until the fruits are fully developed, by which time the enlarged berries push the staminodes upward (Fig. 25H). Shortly after this, the staminodes become much paler and are then shed. This coincides with the now exposed fruits changing from green to yellowish green or yellowish white and rapidly decomposing to a mucilaginous pulp, in which are embedded the green seeds (Fig. 25I).

Dispersal is via a splash-cup mechanism, with water drops striking the inside of the erect persistent funnel-form lower spathe and ejecting the seeds. The seeds, with the aid of the micropylar appendage anchor on the mosses or tiny fissures on the surrounding rock.

In summary, by the time that the interstice staminodes begin to lower, the pistillate flowers are already pollinated and/or the stigmas are no longer receptive. In all observations, interstice staminodes have no function in retaining pollinators inside the spathe during the anthesis transition period, as occurs in numerous unisexual-flowered aroid genera. Rather pollinating insects are attracted in two waves by separate floral odour emissions coinciding with the onset of pistillate and staminate anthesis. The appearance and texture of the post-anthesis staminodes, and their persistence until the mature fruit force their loss, is strongly suggestive of a role protecting the developing fruits. In many respects the interstice staminodes of *Bucephalandra* homeotically fill the role of the sloughing stylar plates of the monstercarp of many *Monsteroideae* (e.g. *Epipremnum* Schott, *Scindapsus* Schott, etc.).

The observations offered here are part of a wider and ongoing study of the biology of *Bucephalandra*. The results from that work are in progress.

Acknowledgements

This study is part of an ongoing research, which is funded by the Ministry of Education Malaysia through Niche Research Grant Scheme vote no. NRGs/1089/2013-

(03) and Fundamental Research Grant Scheme vote no. FRGS/STWN10(01)985/2013(26). Research and fieldwork in Borneo was most recently conducted under Sarawak Forestry Department Research Permit No. NCCD.907.4.4(Jld.9)-69 and Park Permit No 140/2013. The continuing collaboration and support of the Forest Department Sarawak and Sarawak Forestry Corporation are gratefully acknowledged. We wish to extend our thanks to the Directors or Curators of B, BO, FI-B, K, L, M, SAR, and SING for allowing access to material, and to their staff for so helpfully facilitating our observations. We also express our thanks to Wilbert L. A. Hetterscheid for deciphering and translating the Dutch writing on the label of the Kew isotype of *Bucephalandra gigantea*; to Josef Bogner, Hiroshi Okada and Yasuko Mori for permission to reproduce illustrations in Fig. 23; to Nicholas Turland for assistance with the etymology of specific epithets; and to Josef Bogner, David Scherberich and an anonymous reviewer for their comments on an earlier draft of this paper.

References

- Beccari O. 1879: La più piccola delle Aracee. – Bull. Reale Soc. Tosc.ortic. **4**: 179–181.
- Beccari O. 1902: Nelle foreste di Borneo. Viaggi e ricerche di un naturalista. – Firenze: Tipografia di Salvatore Landi.
- Beccari O. [Giglioli E. H. (transl.); Guillemard F. H. H. (ed.)] 1904: Wanderings in the great forests of Borneo. Travels and researches of a naturalist in Sarawak. – London: Archibald Constable & Co, Ltd.
- Bogner J. 1980: The genus *Bucephalandra* Schott. – *Aroideana* **3**: 134–143.
- Bogner J. 1984: Two new aroids from Borneo. – *Pl. Syst. Evol.* **145**: 159–164.
- Bogner J. & Hay A. 2000: *Schismatoglottideae* in Malesia II – *Aridarum*, *Bucephalandra*, *Phymatarum* and *Piptospatha*. – *Telopea* **9**: 183–194.
- Boyce P. C., Bogner J. & Mayo S. J. 1995: *Bucephalandra catherineae*, a new species from Kalimantan. – *Bot. Mag.* **12**: 150–153.
- Boyce P. C. & Wong S. Y. 2012: Studies on *Schismatoglottideae* (Araceae) of Borneo XX: Beccari's «La Più piccola delle Aracee» (*Microcasia pygmaea*) re-collected and transferred to *Bucephalandra* Schott. – *Webbia* **67**: 139–146.
- Engler A. 1879: *Araceae* specialmente Borneensi e Papuane raccolte da O. Beccari. – Bull. Reale Soc. Tosc.ortic. **4**: 295–302.
- Engler A. 1912: *Homalomeninae* und *Schismatoglottidinae*. In: Engler A. (ed.), Das Pflanzenreich. Regni vegetabilis conspectus **55(IV.23Da)**. – Leipzig: Wilhelm Engelmann.
- Grayum M. H. 1992: Comparative external pollen ultrastructure of the *Araceae* and putatively related

- taxa. – Monogr. Syst. Bot. Missouri Bot. Gard. **43**: 1–167.
- Hotta M. 1965: Notes on *Schismatoglottidinae* of Borneo. I. – Mem. Coll. Sci. Kyoto Imp. Univ., Ser. B, Biol. **32**(1): 19–30.
- Mayo S. J., Bogner J. & Boyce P. C. 1997: The genera of *Araceae*. – Kew: Royal Botanic Gardens.
- Okada H. & Mori Y. 2000: Three new species of *Schismatoglottideae*, *Araceae*, from Borneo. – Acta Phytotax. Geobot. 51: 1–9.
- Schott H. 1858: Genera Aroidearum. – Vindobonae: Typis Caroli Ueberreuter.
- Tate R. B. 2001: The geology of Borneo island CD-ROM. – Kuala Lumpur: Persatuan Geologi Malaysia / Geological Society of Malaysia.
- van Steenis C. G. G. J. 1981: Rheophytes of the world: an account of the flood-resistant flowering plants and ferns and the theory of autonomous evolution. – Alphen aan den Rijn & Rockville: Sijthoff & Noordhoff.
- van Steenis C. G. G. J. 1987: Rheophytes of the world. Supplement. – *Allertonia* **4**(Supplement): 267–330.
- Walker A. R. 2005: James Motley (1822–1859). The life story of a collector and naturalist. – *Minerva* [Swansea History Journal] **13**: 20–37.
- Wong S. Y., Boyce P. C., Sofiman Othman A. & Leaw C. P. 2010: Molecular phylogeny of tribe *Schismatoglottideae* based on two plastid markers and recognition of a new tribe, *Philonotieae*, from the neotropics. – Taxon **59**: 117–124.

Index to taxa

Bucephalandra Schott

- Bucephalandra akantha* S. Y. Wong & P. C. Boyce
- Bucephalandra aurantiitheca* S. Y. Wong & P. C. Boyce
- Bucephalandra belindae* S. Y. Wong & P. C. Boyce
- Bucephalandra bogneri* S. Y. Wong & P. C. Boyce
- Bucephalandra catherineae* P. C. Boyce, Bogner & Mayo
- Bucephalandra chimaera* S. Y. Wong & P. C. Boyce
- Bucephalandra chrysokoupa* S. Y. Wong & P. C. Boyce
- Bucephalandra diabolica* S. Y. Wong & P. C. Boyce
- Bucephalandra elliptica* (Engl.) S. Y. Wong & P. C. Boyce
- Bucephalandra forcipula* S. Y. Wong & P. C. Boyce
- Bucephalandra gigantea* Bogner
- Bucephalandra goliath* S. Y. Wong & P. C. Boyce
- Bucephalandra kerangas* S. Y. Wong & P. C. Boyce
- Bucephalandra kishii* S. Y. Wong & P. C. Boyce
- Bucephalandra magnifolia* H. Okada & Y. Mori
- Bucephalandra minotaur* S. Y. Wong & P. C. Boyce
- Bucephalandra motleyana* Schott
- Bucephalandra muluensis* (M. Hotta) S. Y. Wong & P. C. Boyce
- Bucephalandra oblanceolata* (M. Hotta) S. Y. Wong & P. C. Boyce
- Bucephalandra oncophora* S. Y. Wong & P. C. Boyce
- Bucephalandra pubes* S. Y. Wong & P. C. Boyce
- Bucephalandra pygmaea* (Becc.) P. C. Boyce & S. Y. Wong

Bucephalandra sordidula S. Y. Wong & P. C. Boyce

Bucephalandra tetana S. Y. Wong & P. C. Boyce

Bucephalandra ultramafica S. Y. Wong & P. C. Boyce

Bucephalandra vespula S. Y. Wong & P. C. Boyce

Bucephalandra yengiae P. C. Boyce

Microcasia Becc. = *Bucephalandra* Schott

Microcasia elliptica Engl. ≡ *Bucephalandra elliptica* (Engl.) S. Y. Wong & P. C. Boyce

Microcasia muluensis M. Hotta ≡ *Bucephalandra muluensis* (M. Hotta) S. Y. Wong & P. C. Boyce

Microcasia oblanceolata M. Hotta ≡ *Bucephalandra oblanceolata* (M. Hotta) S. Y. Wong & P. C. Boyce

Microcasia pygmaea Becc. ≡ *Bucephalandra pygmaea* (Becc.) P. C. Boyce & S. Y. Wong

Excluded taxa

Microcasia sect. *Truncatae* M. Hotta ≡ *Hottarum* Bogner & Nicolson

Microcasia purseglovei Furtado ≡ *Aridarum purseglovei* (Furtado) M. Hotta

Microcasia truncata M. Hotta ≡ *Hottarum truncatum* (M. Hotta) Bogner & Nicolson