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Colocasia spongifolia sp. nov. (Araceae) in southern China and central Vietnam

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Abstract

Colocasia spongifolia sp. nov. (Araceae) is a large herb in forest edges on mountain slopes in southern China and central Vietnam. The plant is remarkable for its distinct vegetative morphology, while floral morphology places it as a close wild relative of *C. esculenta* (taro), among other closely-related species. The name given here reflects a thick, rubbery, spongy leaf blade unlike the blades in other *Colocasia* species known to us. The blade has exceptionally large spongy mesophyll cavities that are visible to the naked eye. Vegetative reproduction appears to be limited to direct (though shy) sprouting of lateral buds to form new erect stems, without production of side-tubers or stolons. In contrast to other *Colocasia* species, dense spreading colonies (clumps or patches) were not seen.

Keywords: Aroideae, new species, substomatal cavity, marginal vein, peduncle, staminodes, fruit

Introduction

The discovery and present description of *Colocasia spongifolia* (Araceae: Colocasieae) follows our long-term studies of the genus in China and Vietnam, and of *C. esculenta* (Linnaeus 1753: 965) Schott (1832: 18) (taro) in many countries. The known distribution of *C. spongifolia* is restricted to gaps and edges in mountain rainforests along the northeastern edge of the Asian monsoon zone. Although widespread, the plant may have been unremarked until now due to its superficial similarity to wild taro (*C. esculenta*), which is also abundant in Vietnam and southern China. Taro is a globally-distributed root and leaf crop (Matthews & Ghanem 2021) with many distinct clonally-propagated cultivars (Zhu *et al.* 2000, Orchard 2006, Chaïr *et al.* 2016).

Wild species of *Colocasia* Schott (1832: 18) are restricted to damp or wet habitats across the Asian-Pacific monsoonal region, from near sea level to the 3,700 m elevation of *C. gaoligongensis* Li & Long (1999: 423) in Yunnan. Past estimates for the total number of species vary from 8 (Hay 1996) to about 15 (Boyce *et al.* 2012) or 20 (Boyce *et al.* 2011-onwards, Li & Boyce 2010). The diversity of wild *Colocasia* species is greatest in mountainous regions from eastern Himalaya to Vietnam and southern China, and declines to two species in island Southeast Asia (Hay 1996), and a single species (*C. esculenta*) in Australia and Melanesia (Matthews 1991, 2014). Many are known from only brief descriptions and few locations, and some may be synonymous with previously described species (Hay 1996, Li & Boyce 2010, Boyce *et al.* 2012, Gogoi *et al.* 2019). Unknown *Colocasia* species are likely to exist in unexplored regions of monsoonal Asia, and hybridization between species (Matthews 2014, Ahmed *et al.* 2020) has probably also contributed to taxonomic uncertainty. The entire genus requires further exploration, observation and taxonomic revision.

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FIGURE 1. Habit and habitat of *C. spongifolia*. **A**. Single plant ca. 1 m tall, on road bank, at 962 m elevation. **B**. Scatter of adult plants (arrow heads) in upper area of a recent slip face, above road, at 676 m. **C**. Plants collected from roadside at 854 m; blades pale, milky-green on underside. **D**. Same site as B, with young seedling emerging from a bed of moss and liverwort. Photos: PJM.

FIGURE 2. Stem, roots, and buds of *C. spongifolia*. **A**. Cross section of stem in B, showing clear, gummy exudate. **B**. Mature stem with decumbent part at left, erect part at right, roots and rootlets, brown leaf scars, and single adaxial buds (arrows). **C**. Young stem, with single, adaxial bud revealed. Scale bars = 2 cm (Bach Ma NP, 2018, 2021). Photos: NVD and PJM.

In addition to *C. spongifolia*, seven species of *Colocasia* are identified in the key below. This is not a complete set for the genus, but includes most species that are likely to be closely related to *C. spongifolia,* in China and Vietnam. *C. esculenta* is not included because descriptions for this species are based on diverse cultivated and wild plants (Hay 1996, Orchard 2006), and the name has been applied globally to cultivars (diploid and triploid) and wild populations (diploid) that represent three distinct evolutionary lineages (Ahmed *et al.* 2020). The seven species included are:

C. formosana Hayata (1919: 133) (Matthews *et al.* 2015), *C. gaoligongensis*, *C. gongii* Long & Li (2000: 559), *C. kachinensis* Zhou & Yin in Zhou *et al.* (2020: 42), *C. lihengiae* Long & Liu (2001: 313) (Nguyen 2005a), *C. yunnanensis* Long & Cai in Cai *et al.* (2006: 139) (Nguyen *et al.* 2016) and *C. menglaensis* Yin *et al.* (2004: 223) (Nguyen 2005b). Three of these (*C. lihengiae*, *C. menglaensis*, *C. yunnanensis*) are present in Vietnam and China (Nguyen *et al.,* 2016, Nguyen 2017). Li & Boyce (2010) placed *C. gaoligongensis*, *C. gongii* and *C. lihengiae* in *C. antiquorum* (Linnaeus 1753: 965) Schott (1832: 18), and *C. formosana* in *C. esculenta*, a treatment we do not follow. Our key is based on primary and secondary descriptions cited above, and original field observation. Adaxial buds and staminodes have not been described in detail for *C. gaoligongensis, C. gongii and C. kachinensis,* but illustrations in the original reports are informative. The present description of *C. spongifolia* (after key) is based on fresh and preserved, hydrated materials.

Taxonomy

Colocasia spongifolia P.J.Matthews, V.D.Nguyen, Q.Fang & C.L.Long, *sp. nov*. (Figs. 2A, B & 5A, C–I type)

In contrast to *Colocasia esculenta*, *C. formosana*, *C. gongii* and other species, *C. spongifolia* has a thick, rubbery leaf blade with smooth underside (vs thin, not-rubbery, with raised interprimary veins on underside). It differs from *C. esculenta*, *C. formosana*, *C. lihengiae* and other species by having a stem without side-tubers or stolons (vs with side-tubers or stolons) and staminodes absent or rare at base of female zone (vs many or abundant throughout the male zone). It differs from *C. lihengeae*, *C. yunnanensis*, and some cultivars of *C. esculenta* by having a sterile appendix (vs much reduced or absent).

Type:—VIETNAM. Thừa Thiên Huế, Phu Loc, Loc Tri, Bach Ma National Park, on the route from park headquarters to mountain top, and ca. 2 km before the hotel 'Do Quyen Villa'. Elevation 1,201 m. Lat. 16° 11'39.32" N. Long. 107°50'57.54" E; 25th May, 2019, *Nguyen V. D. & Nguyen S. K. 01* (holotype HN!), *Nguyen V. D. & Nguyen S. K. 02* (isotype HN!). A single gathering; each specimen with stem, leaves, inflorescences (no fruit or seeds).

Habit. Medium-sized herb, up to ca. 120 cm height (in open, sunny locations), perennial; usually single, never forming dense spreading colonies (clumps or patches) (Fig. 1). *Stem and roots.* Stem erect, or decumbent with erect apical part; up to 14 cm long and 5.5 cm diam.; adaxial buds single in each leaf axil, rarely forming new stem; side-tubers and stolons absent (Fig. 2). Outer skin surface white, or green on older stems where exposed to light, and covered by fibrous brown remnants of petiole tissue; leaf scars obvious, brown to light brown; inner skin (stem cortex) white; inner parenchyma white, not starchy, exuding clear gum (presumed glucomannan) when cut; roots white (occasionally purple where exposed to light), abundant, up to 25 cm long, 3–4 mm diameter, with many secondary rootlets of ca. 0.4 mm diameter emerging from the primary roots. *Leaves.* Two to several; blade ovate-cordate, peltate, with rounded posterior lobes, shallow sinus, and apiculate anterior lobe; mature blade size highly variable, with a maximum recorded length (from anterior tip to line defined by tips of posterior lobes) of ca. 58 cm, on ca. 116 cm tall petiole; blade waxy (not shining), darker green above, pale or milky green under, anterior lobe tilting down (Figs. 1 & 3). The central veins of the anterior and posterior lobes and the primary lateral veins (pinnate ribs) are raised and pale green on underside; submarginal collective and marginal veins are both distinct, separated by laminal tissue, the former ca. 2–4 mm from edge of blade, the latter close to edge (Fig. 3 A); margins of the posterior lobes fused between each lobe, forming a relatively shallow sinus (deeper in older or larger blades) (Figs 1, 3B). Interprimary (secondary to tertiary) veins are not raised on underside, which is distinctly smooth. Spongy mesophyll envelops the interprimary veins and is thicker next to primary lateral veins (Fig. 3 C, D). In reflected light, underside appears porous with "false pores" where epidermis is clear above mesophyll cavities (Fig. 3 C, D). The blade feels and looks rubbery when touched and bent by hand, forming axial wrinkles (Fig. 3C); milky-green colour of underside is most apparent when light is reflected by the white epidermal layer (Fig. 3C, D). Air cavities in spongy mesophyll (180–360 um diam.) are obvious to eye as lighter spots when viewed from below with light transmitted from above (and none reflecting off the lower surface) (Fig. 3E), or as dark cavities in reflected light when the lower epidermis is peeled away (Fig. 3F). Petiole bright green (pale green or white at base), slender, cylindrical; petiolar sheath extending to 1/2–2/3 of the petiole length; edge of sheath prominent after younger leaf has emerged, but not wide-flaring. *Inflorescence.* Peduncle, 25–30 cm long, cylindrical, upper cross-section sub-triangular (proximal face 8–12 mm across, lateral faces 12–14 mm), medium to light green, covered by one cataphyll up to half of length; erect when young, later bending towards

ground, bringing the fruiting head close to ground or into contact (Fig. 4A). *Spathe* total length up to 19 cm; minimally constricted between lower tube and upper limb; lower tube conical, sub-triangular, 4.5–5.0 cm long, ca. 2.3 cm diam. at base, 1.5 cm diam. at apex, medium green; limb convoluted before opening; nearly oblong when fully open, 11.5–14.0 cm long, 5.0–5.5 cm wide, tip remaining convoluted and acuminate (3 cm long) after opening; yellow to light yellow, with papaya-like scent; upper spathe reflexes after anthesis, away from spadix (Fig. 5A). *Spadix* much shorter than spathe, 10–14 cm long; female (pistillate) zone of young spadix strongly conical, with sub-triangular cross-section (proximal face 10–12 mm across, lateral faces 15–17 mm; similar to upper peduncle), becoming cylindrical at upper end (4.0–4.5 mm diam.); pistils dark green; staminodes absent, or rare at base of female zone; sterile interstice (between male and female zones) constricted or not, 8–15 mm long, upper part ca. 5 mm diam., covered by loosely-spaced synandrodes; male (staminate) zone cylindrical, slightly narrower at upper end, 2.8–3.0 cm long, ca. 5.0–5.2 mm diam., dull yellow; covered closely by male flowers joined in synandria; sterile appendix slender, tapering, 2–3 cm long, ca. 3 mm diam. at base, dull yellow, surface wrinkled (Fig. 5C, D). Ovary sub-globose to cylindrical, cross-section quadrilateral, apex rounded, 1.5 mm tall, 2 mm wide, dark green, glossy; stigma disciform, 4 blunt lobes, sessile, 1-locular; ovules abundant, parietal, orthotropous, ca. 0.3–0.4 mm long (Fig. 5D–G). Staminodes yellow, flask-shaped, smaller than pistil. Synandrodes porcelain-white, flattened, ca. 2 mm thick, outline mostly oblong (Fig. 5C). Synandrium cylindrical, 2 mm tall, 6–8 androus with connate stamens; apical pores 6–8; anther sacs in lateral pairs, each sac with an apical pore; pollen extruded as a loosely self-adhering mass; adjacent synandria appressed with lobes often interlocking (Fig. 5H, I). *Infructescence* (Fig. 5J) composed of lower spathe tube enclosing many green berries (up to ca. 200), berries firm and green when young and expanding, soft and yellow-green to orange at maturity; mature seeds ca. 1.25 mm long, uniform, light brown, oval, pointed at each end, with ca. 12 regular longitudinal ridges; average seed number per berry 40+/–(range 0–60+); total seed number per head up to ca. 8,000.

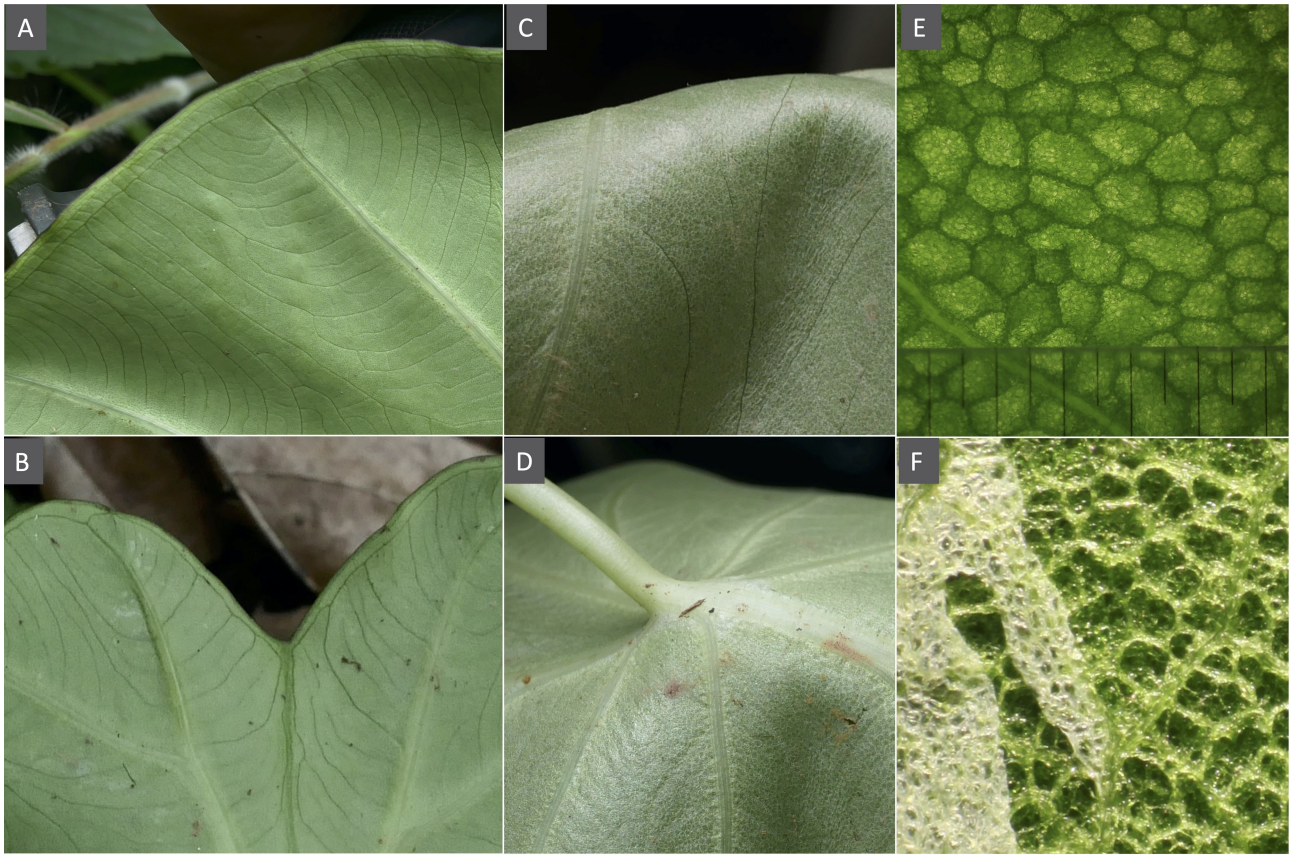

FIGURE 3. Blades of *C. spongifolia*. **A**. Sub-marginal and marginal collective veins, with laminal tissue (2–4 mm) between. **B**. Marginal collective veins fused below shallow sinus. **C**. Underside with spongy appearance produced by "false pores"; and thick, rubbery texture indicated by axial wrinkles formed in crease. **D**. Underside showing primary vein and pinnate lateral veins surrounded by spongy tissue. **E.** Sub-stomatal cavities revealed by transmitted light (scale unit 0.25 mm), **F.** Sub-stomatal cavities revealed by removing lower epidermis (A–D: Mengla County, 2018. E–F: Bach Ma NP seedling, *ex situ*). Photos: PJM.

FIGURE 4. Fruiting heads and peduncles of *C. spongifolia*. **A**. Site WP260; two peduncles have lost heads (arrows 1 and 2), the upper part (male zone) of one spadix lies on ground (arrow 3), and six attached heads all touch ground. **B–E**. Site WP251; a single, detached immature head with bite marks in upper and lower ends, and torn surface at junction with peduncle (at left in D–E). Scale bars: 10 cm with 1 cm units (main image); 8 cm with 2 cm units (lower right); B–C enlarged, without scale. (Bach Ma NP, 2018). Photos: PJM.

Etymology:—The specific epithet is derived from the distinct character of the leaf blade (visibly spongy appearance and rubbery to touch).

Ecology:—In contrast to other *Colocasia* species, dense spreading colonies (clumps or patches) were not seen. The persistent adaxial buds of *C. spongifolia* may support regeneration from fallen, decumbent stems. During *ex situ* cultivation, it has been possible to force buds to sprout by removing the stem apex and placing the stem horizontally on damp soil. At Bach Ma, immature fruiting heads were marked by the teeth of an unknown terrestrial frugivore (possibly a seed disperser, and likely a small mammal), and living larvae of a specialist pollinator (*Colocasiomyia* sp.) were found between berries on mature fruiting heads.

Phenology:—Initial field observations suggest seasonal patterns of flowering, fruiting and seedling growth in relation to rainfall and temperature. Rainfall is generally higher in Thua Thien-Hue than Mengla (Climate-Data.org 2021), peaking in autumn in Hue (600 mm/month, October–November) and summer in Mengla (300 mm/month, July). Maximum daytime temperatures are similar in each area, with hot summers (28–30^0 C) in June–August. In Thua Thien-Hue, we saw early flowering in late May, and late fruiting with mature seeds in late September. These observations indicate a main phase of flowering during the months of peak temperature (May–August), with seed germination and early growth following in wet season. The months of peak temperature and rainfall coincide in Mengla, where young seedlings were seen in early May, at the start of the warm, wet summer. In both areas, wet conditions are likely to favour seedling establishment.

Distribution:—Southern China, Yunnan: Mengla County, Xishuangbanna Dai Autonomous Prefecture, Yunnan, China (several sites NW, NE and SE from Mengla Township). Elevation: 656–962 m; max. straight-line distance between sites: ca. 52 km. Central Vietnam, Thua Thien-Hue: (1) Bach Ma National Park, Loc Tri district, Thua (several sites), (2) vic. Hong Kim, A Luoi District (one site), (3) vic. Huong Nguyen, A Luoi district (several sites). Elevation: 675–1,201 m. Maximum straight-line distance between Thua Thien-Hue sites: ca. 70 km. Max. straight-line distance between northern and southern locations, Mengla to Thua Thien-Hue: ca. 500 km.

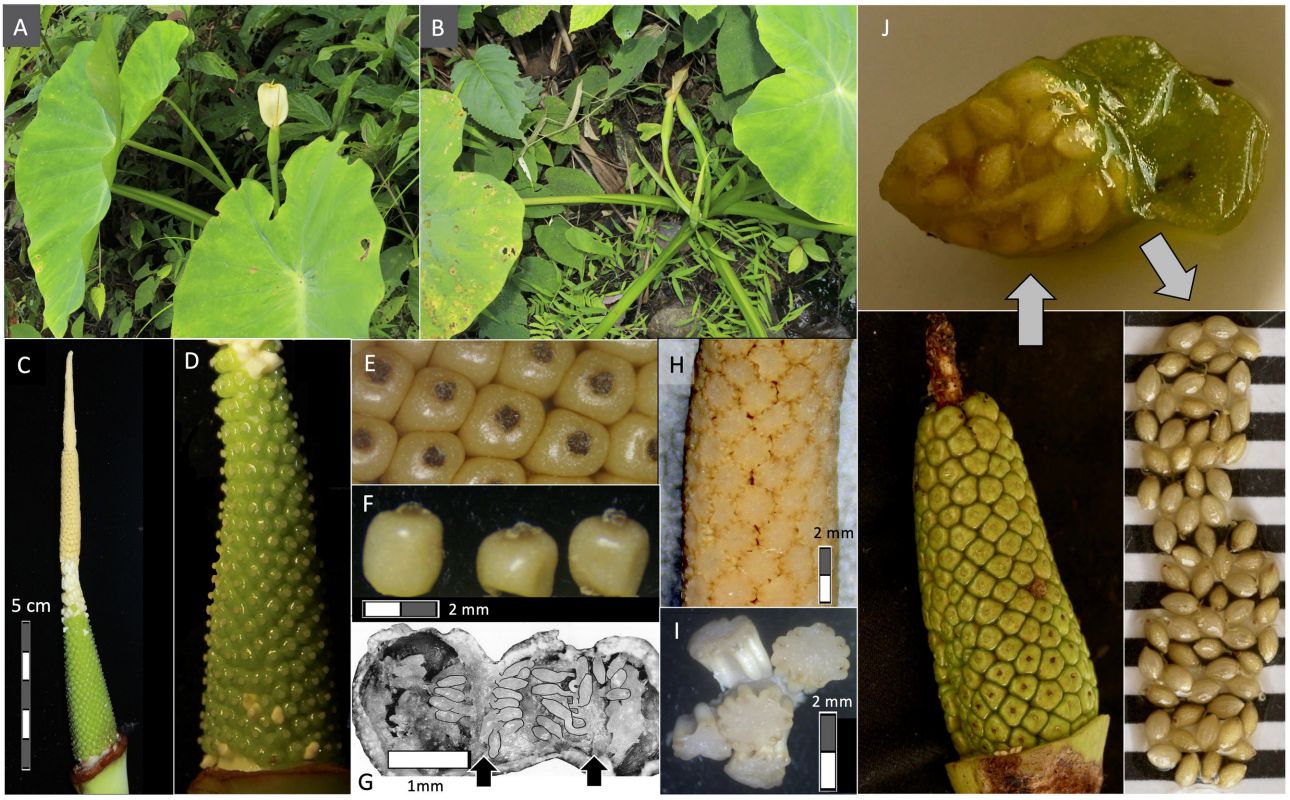

FIGURE 5. Floral habit and structure of *C. spongifolia*. **A**. Type specimen *in situ* with open, spathe limb (apex is reflexed out of view), and green spathe tube (ca. 6 cm long). **B**. Adjacent plant with inflorescences and prophylls. **C**. Spadix showing from top: sterile appendix, staminate (male) zone, sterile interstice, and green pistillate (female) zone with tapered, conical form. **D**. Detail of female zone showing a few basal staminodes. **E–G**. Berries of the preserved type specimen. **G**. Dissected berry with orthotropous ovules (some outlined) attached by funicles to parietal placentae (arrows). **H**. Surface of male zone showing closely-packed synandria. **I**. Synandria separated to show fused anther sacs beneath apical pores (example in center has 8 pores, 8 anthers) **J**. Mature fruiting head, with single berry removed to show seed packing and 67 seeds extracted (scale bar units: 1 mm) (Bach Ma NP; type 2020; fruit and seeds 2018). Photos: NVD and PJM.

Habitat:—Isolated single plants or small populations; usually seen on roadsides but also found distant from road; on humus and colluvium or in rock crevices, in damp to wet positions on moderate to steep slopes with evergreen humid or cloud forest; at forest edge or under canopy gap, with limited direct exposure to sunshine (lower montane environments). The Thua Thien-Hue and Mengla populations occupy a boundary region between the temperate and tropical Köppen-Geiger climate zones defined by Beck *et al.* (2018), namely Cwa/Aw in Mengla, and Cwa/Am in Thua Thien-Hue (Cwa = temperate dry winter, hot summer; Aw = tropical savannah; Am = tropical monsoon).

Conservation:—Common but not abundant in each area of known distribution. Main threat may be loss of forest habitat near roads. Many locations are in conservation areas and appear well protected.

Notes:—The key below keeps the name *C. lihengiae*, though a previously reported Indian representative of this species (Gogoi & Borah 2013) is now recognised as synonym for *C. mannii* Hooker (1893: 524), and is an edible wild leaf vegetable in Assam (Gogoi *et al.* 2019). *C. lihengiae* (c.f. *C. mannii*) may have a complex history if economic use was widespread in the past. In our key, division of *Colocasia* into stoloniferous and non-stoloniferous groups may correspond to previously-suggested acaulescent (often tuberous) and caulescent (erect) sections (Mayo 1997; Krause 1920). Stolons can be easily recognised as present or absent, but when stems are young, short, or often decumbent, it is difficult to classify them as erect or not. Stem position with respect to ground surface often reflects wind, water and soil conditions in sloping, semi-aquatic, or cultivated habitats. Tuberous, stout, erect, decumbent and rhizomatous habits are widespread in Araceae (Mayo *et al.* 1997), so taxa sharing one or more of these morphologies are not necessarily closely related. There might not be any general correlation between stem habit and other traits, though the present key suggests that erect species lack stolons and side-tubers, which in turn may reflect shy sprouting by adaxial buds. Erect stems with condensed nodes (where adaxial buds are located) are common in the sub-family Aroideae to which *Colocasia* belongs, and are found in *Alocasia* and *Steudnera*, for example (Mayo *et al.* 1997).

Four characters described here for *C. spongifolia* have not been described in detail in previous reports of *Colocasia* species: margination of the leaf blade, spongy mesophyll cavity dimensions in the leaf blade, adaxial buds (including their abundance within an axil, and their development into lateral shoots), and peduncle orientation at the time of fruiting. All of these may be ecologically significant characters and require further study across the genus. Notes for each character follow.

(1) Leaf margination varies greatly in aroids generally (Mayo *et al.* 1997). Among *Colocasia* species we see a marginal vein compression series (forms i-iv), with two marginal vein types located near or compressed at the edge: (i) No obvious marginal vein or submarginal collective vein (both types apparently fully merged into the blade edge). (ii) A submarginal collective vein near the edge, with no obvious marginal vein. (iii) A sub-marginal collective vein slightly separate from an inconspicuous marginal vein near the edge. (iv) A sub-marginal collective vein clearly separated by laminal tissue from an obvious marginal vein near the edge. Forms i–iii are found in other *Colocasia* species, while iv is typical in *C. spongifolia*, in wild plants and seedlings *ex situ*.

(2) Few data are available on spongy mesophyll cavity dimensions in *Colocasia*. Our own initial observation indicates an approximate range of 100–200 um diam. in planar view (after peeling off the lower epidermis) of a single, fresh sample of cultivated *C. esculenta*, and 180–360 um diam. in *C. spongifolia*. Keating (2002: 285) shows micrographs of similar, large substomatal air spaces in the spongy mesophyll of *C. fallax*, using thin sections of chemically-fixed tissue, but the dimensions in fresh and fixed tissues may not be comparable.

(3) In seedlings observed *ex situ*, over a period of three years, the adaxial buds in *C. spongifolia* have been consistently single and non-sprouting, with removal of the apical shoot needed to force sprouting and production of a new erect stem. Over the same period in the same location, and without removal of the apical shoot, *C. formosana* produced abundant long stolons, as it does in the wild. Bud behaviour (whether shy or readily sprouting) may be independent of whether or not adaxial buds are single or multiple in leaf axils. Further study is needed to understand the relationship between lateral bud abundance, lateral shoot absence or presence, and the overall growth habits of *Colocasia* species.

(4) Peduncles in *C. spongifolia* show strong downward bending (geotaxis) that begins during anthesis and continues as the upper spathe withers. In wild plants, mature fruiting heads were bent low to the ground or were missing (perhaps removed by terrestrial frugivores) (Fig. 4). The bending behaviour was also observed *ex situ* in potted seedlings that flowered and fruited after self-pollination. Peduncle orientation when fruit reach maturity has not been reported for most *Colocasia* species, but the mature fruit of *C. esculenta* are generally displayed on erect peduncles.

Identification key

1. Plants with stolons; stem short to tuberous and decumbent, or rhizomatous; with multiple adaxial buds in each leaf axil; spadix with sterile appendix or not; staminodes between ovaries many to abundant 2
- Plants without stolons or side-tubers; stem cylindrical, erect; a single adaxial bud in each leaf axil; spadix always with sterile appendix; staminodes between ovaries few or absent 6
2. Sterile appendix long (up to ca. 10 cm, > 2x length of male zone), thick, diam. up to 10 mm at base (wider than male zone) ..... *C. formosana*
- Sterile appendix short and slender, much reduced, or completely absent 3
3. Sterile appendix short (length 3.5 cm, equal to male zone), slender conical, diam. 5 mm at base (more narrow than male zone); underside of leaf blade surface pilose, main and primary lateral veins pubescent; petiole and peduncle pubescent ..... *C. menglaensis*
- Sterile appendix absent or much reduced; underside of leaf blade pubescent over whole surface, or not; petiole and peduncle not pubescent 4
4. Plant stout, petiole maximum 55 cm long; stem short (<2 cm long, 3 cm diam.; sub-globose); inflorescence appears with leaves; peduncle little shorter than petiole ..... *C. gaoligongensis*
- Plant tall, 50–100+ cm long; stem sub-globose to elongate, decumbent, minimum 2 cm long; inflorescences appear after leaf emergence; peduncle much shorter than petiole 5
5. Blade cordate-ovate, upper surface waxy, not glossy green, often with dark purple patches; interprimary veins very prominent on underside of mature blade; sterile appendix absent (a much reduced vestige, apiculate, < 1cm); staminodes between ovaries abundant, with flask shape and discoid apex ..... *C. yunnanensis*
- Blade cordate-sagittate, overall elongate-triangular with deep sinus, upper surface not waxy (wettable), glossy green, without purple patches; interprimary veins inconspicuous to slightly raised on underside of mature leaf; sterile appendix completely absent; staminodes between ovaries abundant, obovate with rounded apex ..... *C. lihengiae*
6. Leaf blade oblong-ovate, posterior lobes narrow and rounded; underside of blade pubescent over whole surface, including primary veins; peduncle cylindrical ..... *C. kachinensis*
- Leaf blade cordate-ovate; posterior lobes broad and rounded; no parts pubescent; peduncle three-angled 7
7. Plant very large, petiole 90–140 cm; stem erect or nearly erect, 120–135 cm long, 12–18 cm diam.; leaf blade with distinctly indented sinus, main vein and primary lateral veins purple, lamina “membranous”; peduncle green or purple; spathe ca. 33 cm

long, spathe blade yellow with purple margin, almost erect or sometimes reflexing at anthesis; spadix ca. 30 cm long, little shorter than spathe ..... *C. gongii*

- Moderate sized plant, petiole up to 120 cm, stem erect or decumbent with erect apex, up to 14 cm long, 5.5 cm diam.; leaf blade with shallow sinus, main vein and primary lateral veins green; lamina thick, rubbery, smooth on underside; peduncle green; spathe up to 19 cm long, spathe blade yellow without purple margin, strongly reflexed at anthesis; spadix 10–14 cm long, much shorter than spathe ..... *C. spongifolia*

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