

The genus *Hapaline* (Araceae: Aroideae: Caladieae)

P. C. BOYCE

Summary. The history, nomenclature, classification and relationships of the genus *Hapaline* (Araceae) are discussed. Seven species, one, *Hapaline celatrix*, new to science, are described and illustrated and a key is provided.

INTRODUCTION

Hapaline is a genus of seven species occurring from Burma (Myanmar) and China (Yunnan) to Brunei. Schott (1857) published *Hapale* for a small, tuberous-stemmed herb collected by Wallich in Burma almost 30 years earlier. Later, Schott (1858) altered the generic spelling to *Hapaline* to prevent confusion with the zoological *Hapale* Illiger (1811), a genus of South American marmosets. Nicolson (1981) pointed out that under Principle 1 of the International Code of Botanical Nomenclature (Stafleu *et al.* 1978) 'Botanical nomenclature is independent of Zoological nomenclature' and that the name *Hapaline* was illegitimate (superfluous) under Art. 63.1 of the Leningrad Code (Stafleu *et al.* 1978) (= Art. 52.1 of the Tokyo Code, Greuter *et al.* 1994)). However, taxonomists had universally adopted the name *Hapaline*. The matter was resolved by the conserving of *Hapaline* over *Hapale* (Eichler *et al.* 1984, Greuter *et al.* 1988).

CLASSIFICATION AND RELATIONSHIPS

Hapaline has always occupied an anomalous position in the various proposed aroid classifications. Schott (1860) produced a family classification based primarily on floral characters. Paleotropical *Hapaline* was placed in the otherwise neotropical subtribe *Syngoninae* of tribe *Caladieae* (including *Caladium* Vent., *Syngonium* Schott and *Xanthosoma* Schott); evidently he had realised *Hapaline* was rather different from the palaeotropical genera of his tribe *Caladieae*. Engler (1876a, 1876b), working mainly with vegetative characters, redefined tribe *Caladieae* of his subfamily *Colocasioideae*, removing all but *Caladium* and *Xanthosoma* and not suggesting a placement for *Hapaline*. Engler (1879) expanded on this arrangement, including all genera known to him, and placed *Hapaline* in tribe *Caladieae*. Engler maintained this classification for *Natürlichen Pflanzenfamilien* (Engler 1889) but by 1920 had reconsidered the generic position of *Hapaline* and recognized a new monogeneric subtribe, *Hapalininae*, (tribe *Colocasieae*: subfamily *Colocasioideae*), to emphasize the apparent isolation of the genus (Engler & Krause 1920). Grayum (1990) produced a classification based on a wider range of characters but retained *Hapaline* in much

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¹The Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AE, U.K.

the same position as Engler. Bogner & Nicolson (1991) produced an essentially updated Englerian classification and did not alter the position of *Hapaline* from that of Engler (1920).

Recently Mayo *et al.* (in press) have undertaken a cladistic analysis of the *Araceae* as part of the 'Genera of *Araceae*' project. This has radically altered the topography of Engler's suprageneric family classification. Some of Engler's subfamilies, including the *Colocasioideae*, have been dismantled. *Hapaline* is assigned to *Caladieae*, one of two tribes in the '*Caladium* alliance'. Besides *Hapaline*, tribe *Caladieae* contains all the neotropical genera recognized by Engler in his subfamily *Colocasioideae*. The other palaeotropical genera of Engler's *Colocasioideae* are placed in *Colocasieae*, one of 15 tribes for which no alliance has been established.

CHARACTERS USED TO DETERMINE GENERIC PLACEMENT

Although *Hapaline* is entirely palaeotropical in distribution, its morphology, cytology, anatomy and biochemistry indicate a close relationship to neotropical genera. Grayum (1984, 1990) cited seven characters that separate *Hapaline* from other palaeotropical 'colocasioid' genera (e.g. *Ariopsis* Nimmo, *Remusatia* Schott and *Colocasia* Schott) (Table 1). Some of these characters are now known to occur sporadically in other paleotropical genera (Hay pers. comm.) but nowhere except *Hapaline* do they occur as a suite. Grayum's second character (Absence of sympodial branching in the terminal reproductive shoot) is unreliable and should be deleted from the list; synflorescences do occur in *Hapaline*.

French & Tomlinson (1983) and Fox & French (1988) demonstrated that the permanent cortical vascular system typical of neotropical 'colocasioids' (excluding *Jasarum* Bunting) and absent from palaeotropical genera, is present in *Hapaline*. Further evidence of a neotropical link was presented by French & Fox (in prep.) who found that the white latex secreted from cut tissue of *Hapaline* is similar in composition to that found in neotropical *Caladieae* and unlike that of palaeotropical genera in the *Colocasieae*.

Palynological evidence for an alliance between *Hapaline* and neotropical genera is less convincing. *Hapaline* pollen has spinose exine sculpturing, a character shared

TABLE 1. Characters separating *Hapaline* from other palaeotropical 'colocasioid' genera (after Grayum, 1990). Comments in [] are additional to Grayum's original list.

1. Non-peltate leaves (relatively rare in palaeotropical genera) [but cf. *Alocasia*]
2. Spathe-spadix fusion [cf. *Alocasia aequiloba* N.E.Br.]
3. Uniovular ovaries.
4. Base chromosome number of $x = 13$ ($x = 14$ in rest of *Caladieae*).
5. Trinucelate pollen (but also present in *Remusatia* Schott).
6. Sterile male flowers above and below the fertile male flowers [cf. *Alocasia*, many species with staminodial appendages]

by almost all other palaeotropical 'colocasioids' (except *Steudnera* Schott and some *Colocasia* spp.), but occurring only in neotropical *Syngonium* (Grayum 1984, 1990, 1992). However, Grayum (1984) noted that the trinucleate pollen of *Hapaline* was similar only to *Remusatia* among the palaeotropical 'colocasioid' genera.

An interesting hypothesis put forward by Grayum (1984) was that *Hapaline* might be related to *Pinellia* Tenore in tribe *Areae* (subfamily *Aroideae sensu* Grayum 1984 (= subfamily *Aroideae*: tribe *Arisaematae* *sensu* Mayo *et al.*, in press)). This is based on the shared characters of tuberous habit, fusion of the base of the spathe and spadix, sterile male flowers or naked regions above and below the fertile male flowers, unilocular, uniovular ovaries, anatropous ovules, endospermous seeds, inaperturate, globose, spinose, starchy, trinucleate pollen and a base chromosome number of $x = 13$. However, *Hapaline* and *Pinellia* differ in a number of fundamental characters, including venation ('colocasioid' versus reticulate), stamen type (synandria versus free) and secretion tubes (present versus absent). Grayum concluded that although it was conceivable that *Hapaline* might be moved to tribe *Areae*, for the time being it was best left in subfamily *Colocasioideae* (*all sensu* Grayum 1984).

MORPHOLOGY AND DISTRIBUTION

Habit and stem

All species of *Hapaline* are diminutive to moderate-sized slender to slightly robust tuberous or stoloniferous, clump-forming terrestrial herbs. Tuberous-stemmed species often produce slender, cataphyll-encased stolons that eventually give rise to new tubers.

Leaf

Leaf blades in *Hapaline* are either thin-textured or thick and leathery. They vary in shape from ovate to hastate. Posterior lobes are present in all species, although lacking from some individuals of *H. appendiculata* Ridl. (see below). The arrangement of the posterior lobes ranges from being parallel in *Hapaline ellipticifolia* C.Y. Wu & H. Li, resulting in an elliptic leaf blade, to hastate in *H. colaniae* Gagnep.

Hapaline displays two distinct growth types which are linked to the thickness of the leaf blades. Species with thin-textured leaf blades (i.e. *H. benthamiana*, *H. brownii*, *H. colaniae*, *H. ellipticifolia* and *H. kerrii*) undergo an annual dormant period. These species occur in areas with a seasonal climate (e.g. Burma, central and NE Thailand, northern Peninsular Malaysia, much of Vietnam). New growth is marked by leaf emergence and abundant flowering.

Species with thicker, leathery leaves, (*H. appendiculata* and *H. celatrix*), do not undergo a dormant period. They are native to areas with a more-or-less aseasonal climate (e.g. Sarawak and Brunei). These differences, coupled with floral morphology characters, define what appears to be a natural division into two groups of allied species: *H. appendiculata* and *H. celatrix* and *H. benthamiana*, *H. brownii*, *H. ellipticifolia*, *H. colaniae* and *H. kerrii*.

Leaf blade variegation, in the form of irregular and diffuse silver grey to pale green blotches, has been reported in *H. appendiculata*, *H. benthamiana*, *H. brownii* and *H. colaniae*.

Inflorescence

All *Hapaline* species have white spathes occasionally tinged green or greyish pink. The spathe is always divided into two zones with the upper part flattened and erect to reflexed and the lower part clasping. The inflorescence is borne on a short to long, green to grey-pink mottled peduncle. At anthesis the peduncle is more-or-less erect to nodding. After fertilization it thickens and bends downwards, bringing the developing fruits to soil level. The spathe persists, the limb eventually breaking off or rotting away to leave the clasping lower spathe enclosing the ripening fruit (Fig. 2, G; Fig. 3 J).

The spadix is bisexual with unisexual, naked flowers. The ovary consists of an ellipsoid, ovoid or bottle-shaped uniloculate, uniovulate ovary with a single anatropous ovule on the basal end of a parietal placenta. The positioning of the ovules results in an ovule that is functionally basal. The staminate flowers are 3-androus and fused into somewhat scattered to densely aggregated, peltate, synandria. The connectives are massively enlarged into a mushroom-like structure with the thecae inserted on the lower margin of the connective apex and dehiscing by an ovate pore (Fig. 3, G & H; Fig. 5, F & G). The male and female zones are separated by a few synandrodes. All species have a further zone of synandrodes situated at the spadix apex. In *H. appendiculata*, *H. brownii* Hook.f. and *H. celatrix* P.C. Boyce the spadix apex is enclosed by a cap formed of fused synandrodes; in the other species the synandrodes are free. A perfume has been reported from cultivated specimens of *H. kerrii* Gagnep. (*Collins* s.n. sub. *Kerr* 19462, K!) and faint but very pleasant perfumes are detectable from cultivated plants of *H. benthamiana* Schott, *H. brownii*, *H. colaniae* and *H. celatrix* (Boyce & Hay pers. obs.). No pollination studies have been undertaken.

Infructescence

Infructescences are known for five species (*H. appendiculata*, *H. benthamiana*, *H. brownii*, *H. celatrix* and *H. colaniae*). The berries are enclosed in the persistent lower spathe remains until maturity (Fig. 2, G; Fig. 3 J). When ripe the berries are globular to ellipsoid with slight to rather prominent stigmatic remains. The pericarp is leathery and the mesocarp sticky. Ripe berries are white and contain a single seed. The seeds are generally ellipsoid with a very thin smooth testa and a conspicuous raphe. The embryo is large, has a conspicuous plumule and lacks endosperm (Seubert 1993: 218 – 219). The ripe infructescence is held at soil level by the thickened and reflexed peduncle (see above). The method of seed dispersal is unknown.

Distribution

Hapaline species occur from Burma to southwestern China (Yunnan) and as far south as Brunei. Most species are quite rare, usually occurring as scattered colonies or occasionally individual plants. In Brunei, *H. celatrix* occurs as large isolated patches at the edge of lowland mixed dipterocarp forest. In Thailand, *H. benthamiana* occasionally occurs as extensive colonies formed as the result of its stoloniferous habit.

THE GENUS *Hapaline* Schott

Hapaline Schott, Gen. Aroid. 44, t.44 (1858) *nom. cons.* (see Nicolson 1981, Eichler *et al.* 1984) & Prodr. syst. Aroid. 161 – 62 (1860); Benth. & Hook. f., Gen. Pl. 3(2): 977 – 78 (1883); Engler in A. & C. DC., Monogr. Phan. 2: 489 – 90 (1879) & in Engler & Prantl (eds), Nat. Pflanzenfam. 2(3): 139 (1889); Engler & Krause in Engler (ed.), Pflanzenr. 71 (IV.23F): 21 – 22 (1920); Hook.f., Fl. Brit. India 6: 521 (1893); Ridley, Fl. Mal. Penins. 5: 95 – 6 (1925); Gagnepain in Notul. Syst. 9: 116 – 40 (1941) & in Lecomte (ed.) Fl. Gén. l'Indo-Chine 6: 1130–1132 (1942); Hu in Dansk. Bot. Ark. 23: 426 – 27. (1968); Bogner in Pl. Syst. Evol. 144: 59 – 66 (1984)

Hapale Schott in Oesterr. Bot. Wochenschr. 7: 85 (1857), *in syn., nom. rejic.* (see Nicolson 1981, Eichler *et al.* 1984).

Diminutive to moderately sized, slender to slightly robust, tuberous to stoloniferous-stemmed, clump-forming perennial evergreen or deciduous herbs to 30 cm tall. **Stem** tuberous to stoloniferous, eventually clustering, stolon slender, encased by several cataphylls. **Roots** slender, little branched. **Leaves:** *prophyll* tubular; *cataphyll* oblong-lanceolate to linear-triangular or triangular, apex attenuate to acute; *petiole* terete, slender; *leaf blade* ovate to sagittate to hastate, light to dark green, occasionally with silver-grey to pale green diffuse markings. **Inflorescence** emerging before, with, or after the leaves, 3 – many together, carried below, level with or above the foliage; *peduncle* terete, slender, shorter than to exceeding petiole; *spathe limb* elliptic to lanceolate, apex acute to briefly attenuate; *lower spathe* margins clasping; *spadix* with female zone adnate to spathe, male and sterile zones free, cylindric to fusiform, tapering apically into an attenuated to short sterile appendix composed of fused or free synandrodes. **Flowers** unisexual, naked; *synandria* irregularly linear-elongate to oblong in plan view, apex flat, connectives massively enlarged into mushroom-like structures, thecae roundish, inserted on the lower margin of the connective apex, dehiscing by an ovate pore; *ovary* bottle-shaped to ellipsoid; *stigma* capitate, papillose; *style* absent to rather pronounced. **Infructescence** partially to completely enclosed by the persistent lower spathe, few-berried; *berries* globular to ellipsoid usually with persistent stigmatic remains, pericarp leathery, white, mesocarp sticky, whitish; *seed* ellipsoid with a very thin smooth testa and a conspicuous raphe, embryo large, plumule conspicuous, seed lacking endosperm. Type species: *Hapaline benthamiana* Schott.

Seven species ranging from Burma to China (Yunnan) and south to Brunei.

KEY TO THE SPECIES OF *Hapaline*

1. Spadix with sterile apex formed of fused synandrodes 2
- Spadix with sterile apex formed of free synandrodes 4
2. Spadix sterile apex greatly elongated, exceeding spathe limb
 1. *H. appendiculata*
- Spadix sterile apex not greatly elongated, not exceeding spathe limb 3

3. Whole plant never more than 5 cm high. Inflorescences borne on short peduncles beneath the foliage; spadix c. 1 cm long **2. *H. celatrix***
Whole plant generally more than 5 cm high. Inflorescences borne above the foliage; spadix 5 – 8 cm long **3. *H. brownii***
4. Leaf blade broadly elliptic-cordiform; ovary solitary **4. *H. kerrii***
Leaf blade sagittate, hastate or elliptic; ovaries 7 – 8 **5**
5. Leaf blade hastate, strongly constricted above the posterior lobes
. **7. *H. colaniae***
- Leaf blade variably sagittate or elliptic, not or barely constricted above the posterior lobes **6**
6. Leaf blade variably sagittate, occasionally constricted at the junction of the anterior and posterior lobes, posterior lobes divergent; ovary ovoid
. **5. *H. benthamiana***
- Leaf blade elliptic, never constricted at the junction of the anterior and posterior lobes, posterior leaf lobes not divergent; ovary bottle-shaped
. **6. *H. ellipticifolia***

1. *Hapaline appendiculata* Ridl. in J. Straits Branch Roy. Asiat. Soc. 49: 47 (1908 ('1907')); Bogner in Pl. Syst. Evol. 144: 62 (1984). Type: Sarawak, Ridley 12411 (holotype SING!; isotype K!).

Slender, tuberous, evergreen perennial herb up to 20 cm high. **Stem:** *tuber* cylindric, 1.5 × 1 cm; *stolon* unknown. **Roots** c. 0.25 – 0.33 mm in diam. **Leaf:** *prophyll* linear, up to 9 × c. 4 mm, acute; *cataphyll* oblong-lanceolate to linear triangular or triangular, up to 10 cm × 5 mm, attenuate to acute; *petiole* 2.5 – 12 cm × 1 – 2 mm; *leaf blade* ovate to hastate to subsagittate, 10 – 16 × 3.5 – 6.5, coriaceous, light to dark green, occasionally with pale green diffuse markings, cm, margins smooth, apex acuminate, posterior lobes rounded to subacute, divergent to almost parallel, rarely absent. **Inflorescence:** 3 – 4 together; *peduncle* 4 – 10 cm × 0.25 – 0.5 mm; *spathe* 2 – 3 cm long; *spathe limb* elliptic, 1.6 – 2.6 cm × 5 – 7 mm, apex acute to briefly attenuate, base decurrent into lower spathe; *lower spathe* margins clasping, 4 – 8 × c. 1.5 mm; *spadix* 2.5 – 3.5 cm × 0.25 – 1 mm, free portion cylindric, up to 8 cm long, tapering apically into an greatly attenuated appendix composed of fused synandrodes. **Flowers:** *synandria* irregularly elongate in plan view, 2 – 3 × 0.5 – 1 mm; *ovaries* bottle-shaped, 1.5 × 0.7 mm, 2 – 3 in a single row; *stigma* capitate, c. 0.2 mm in diam., papillose; *style* very short. **Infructescence:** enclosed by the persistent lower spathe, 2 cm × 4 mm, few-berried; *berries* more or less globular, c. 4 mm in diam, stigmatic remains persistent, not prominent. (Fig. 1).

DISTRIBUTION. Malaysia (Sarawak).

SARAWAK. 1st Division: Bau, Bidi, 6 Dec. 1905, Hewitt 476 (K (photo!), SING!). 7th Division: Belaga Distr., Punan Lusong to Long Jakah, 8 Sept. 1978, Burtt & Woods 11477 (E!); Puak, Sept. 1890, Ridley 12411 (holotype SING!; isotype K!).

HABITAT. In humus at path side on basalt.

Hapaline appendiculata appears to be one of the rarest aroids in Borneo, with only four collections known to date. One of these, made by Anderson near Bau in the 1st

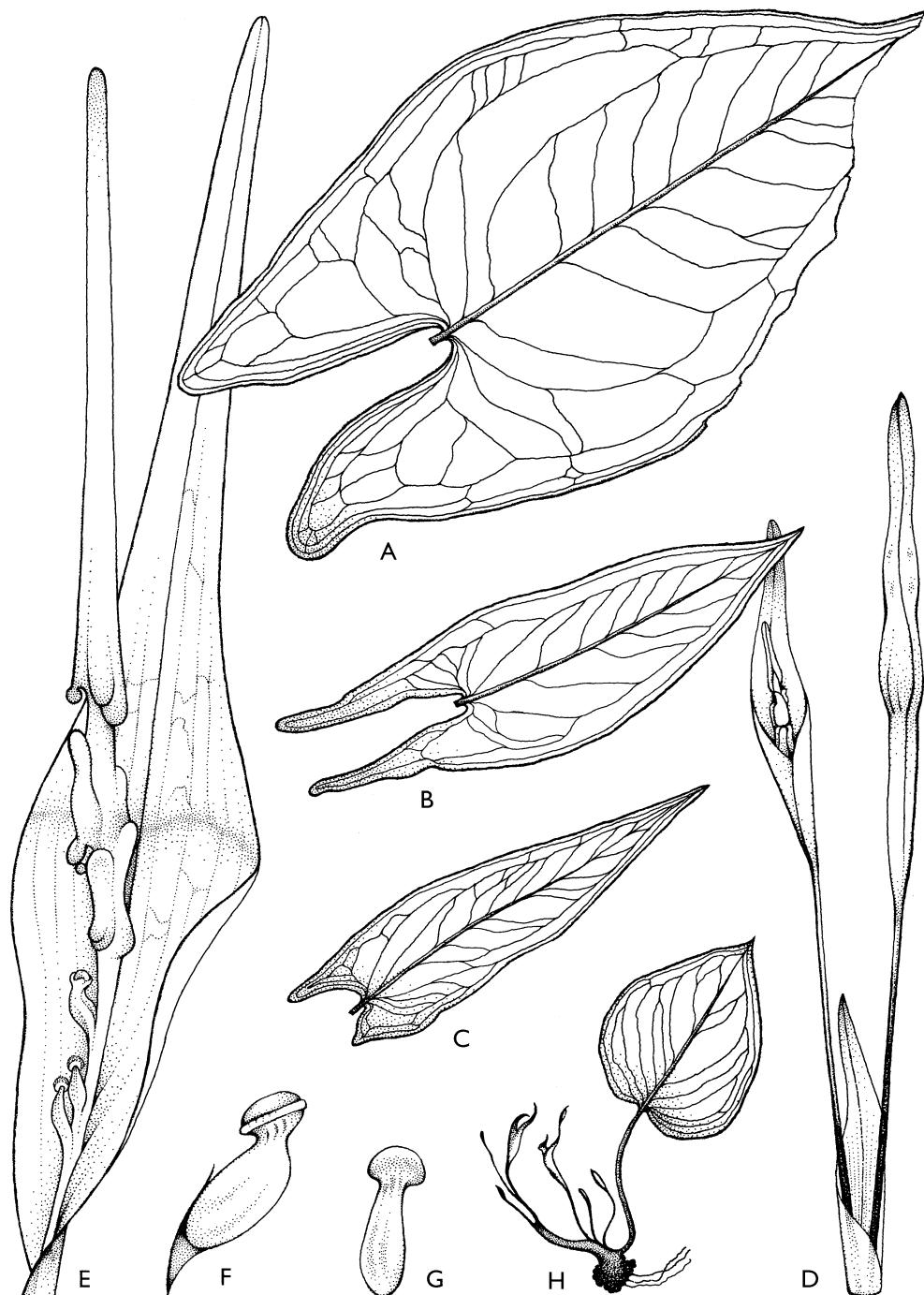


FIG. 1. *Hapaline appendiculata*. A - C leaf shape variation $\times 1\frac{1}{2}$; D flowering shoot $\times 1\frac{1}{2}$; E inflorescence $\times 4$; F ovary, side view $\times 16$; G ovary, rear view $\times 16$; H whole plant of entire-leaved form $\times 1\frac{1}{2}$. A - G from Ridley 12411; H from Hewitt 4760. Drawn by Emmanuel Papadopoulos.

Division of Sarawak, was later cultivated at Singapore Botanic Gardens and noted to have variegated leaves. Herbarium material of this collection was never prepared (Bogner 1984).

Hapaline appendiculata is allied to *H. celatrix* in having evergreen coriaceous leaves and a terminal sterile appendix composed of fused synandrodes. In *H. appendiculata* this sterile appendix is greatly extended into a tail-like process.

One of the cited collections (Hewitt 476) has ovate leaf blades lacking posterior lobes. Study of the inflorescences reveals no significant floral differences from typical *H. appendiculata*. Given the paucity of *H. appendiculata* collections I am not attaching any taxonomic significance to this vegetative variation.

2. *Hapaline celatrix* P.C. Boyce sp. nov., *H. celatrix* ab omnibus aliis speciebus generis concursu habitus semperfurentis, inflorescentiarum parvarum sub frondibus portatarum et inopiae appendicis valde elongati sterilis spadicis distinguibilis. *H. appendiculatae* et *H. brownii* in aspectu toto simillima est. Ab illa inopia appendicis valde elongati sterilis spadicis inflorescentiis minoribus distingui potest, et ab hac inflorescentibus minoribus sub frondibus portatis differt. Typus: Boyce 417 (holotypus K!; isotypi BRUN!, L!, K! (siccus et spiritus sub. num. Kew. 57283), SING!).

[*Hapaline celator* P.C. Boyce in Hay *et al.* in Blumea suppl. 8: 68 (1995), *nom. nud.*]

Diminutive, tuberous, evergreen perennial herb up to 5 cm high. **Stem:** *tuber* globose, 7 – 17 × 7 – 13 mm; *stolon* terete, 1 – 4 cm × 2 – 4 mm, enclosed by several papery cataphylls. **Roots** c. 0.2 mm in diam. **Leaf:** *prophyll* linear-triangular, up to 9 cm × 5 mm, acute to apiculate; *cataphyll* linear-triangular, up to 12 cm × 9 mm, attenuate to rather blunt; *petiole* 8 – 9 cm × 0.5 – 1.5 mm; *leaf blade* cordiform, 5.5 – 16 × 2.7 – 10.5 cm, thickly coriaceous to almost succulent, dark green, margins smooth, apex acuminate, posterior lobes rounded, divergent to sub-parallel. **Inflorescence:** solitary to several together; *peduncle* 3 – 6 cm × 0.5 – 2 mm; *spathe* 1.5 – 2 cm long; *spathe limb* elliptic, 1.5 – 2 cm × 6 – 10 mm, apex acute, base decurrent into lower spathe; *lower spathe* margins clasping, 1.5 – 3 cm × 2 mm; *spadix* 1 cm × 2.5 – 3 mm, free portion narrowly conic, c. 8 mm long, tapering apically in to a stout conical appendix composed of fused synandrodes. **Flowers:** *synandria* irregularly elongate in plan view, 2 – 7 × 0.75 – 1.5 mm; *ovaries* ellipsoid, 2 – 2.5 × 0.5 – 1 mm, 2 – 4 in a single row; *stigma* slightly prominent, c. 0.2 mm diam; *style* absent. **Infructescence:** partially enclosed by the persistent lower spathe, few-berried; *berries* ellipsoid to almost globose c. 3 mm in diam., stigmatic remains persistent, slightly prominent. (Fig. 2.).

DISTRIBUTION. Brunei.

BRUNEI. Temburong: Sungai Temburong at Kuala Belalong, 4°32' N, 115°9' E, 20 June 1989, Boyce 358 (BRUN!, K!); Sungai Temburong at Kuala Belalong, banks of Sungai Belalong. 4°32' N, 115° 9' E, 24 June 1989, Boyce 417 (holotype BRUN!; isotypes K!, K spirit 57283!, L!, SING!).

HABITAT. Disturbed mixed dipterocarp forest on river banks, Setap shales; 20 m.

Hapaline celatrix differs from all other species by the combination of evergreen habit, small inflorescences borne beneath the leaves and a sterile spadix appendix.

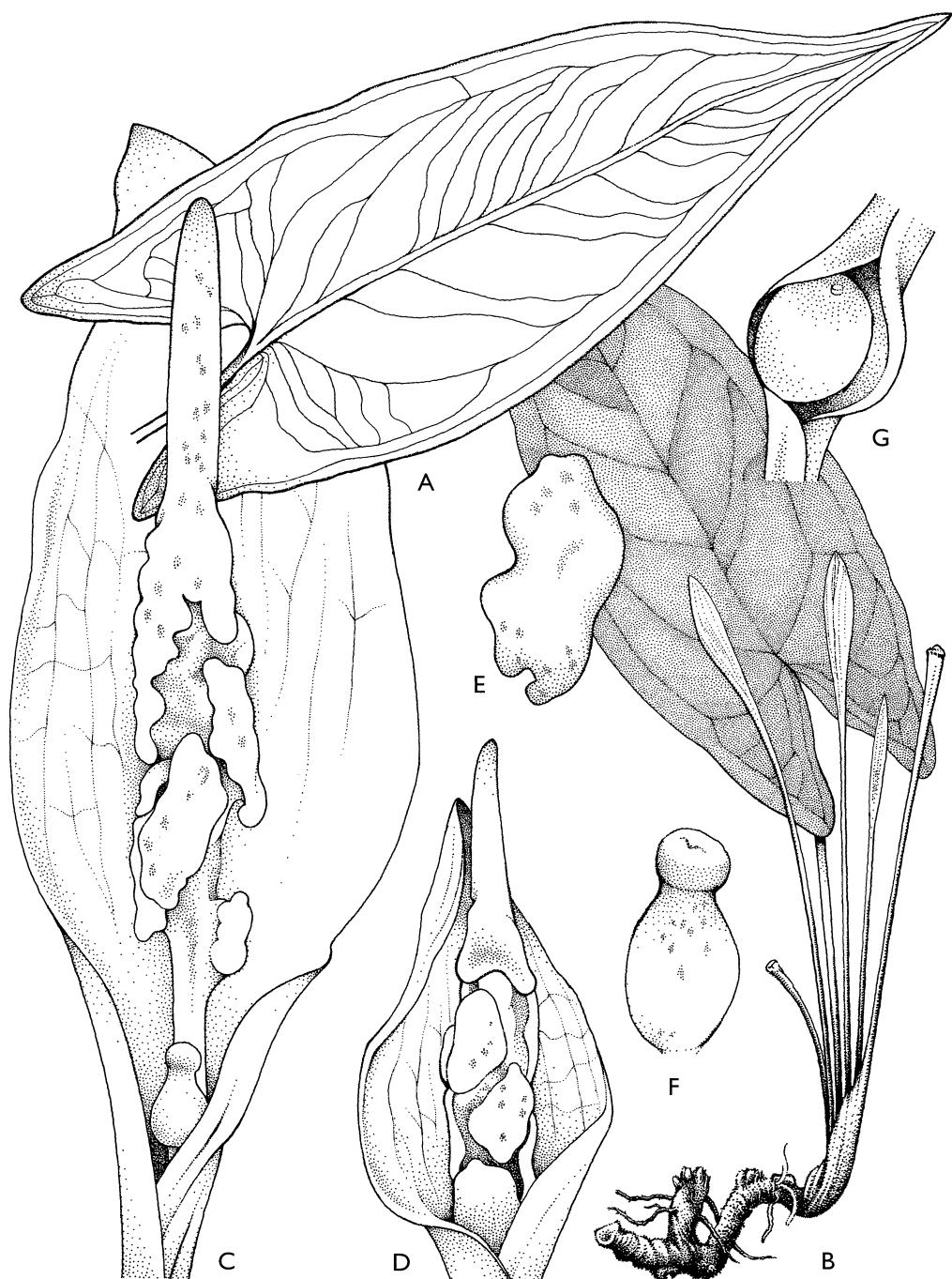


Fig. 2. *Hapaline celatrix*. **A** leaf $\times 1$; **B** whole plant flowering $\times 1$; **C** inflorescence $\times 6$; **D** inflorescence to show variation in sterile appendix $\times 4$; **E** synandrium, plan view $\times 10$; **F** ovary, side view $\times 14$; **G** ripe infructescence $\times 3$. Drawn from Boyce 417 by Emmanuel Papadopoulos.

It is most similar to *H. brownii* and *H. appendiculata*. It may be distinguished from *H. brownii* by the its overall lesser stature and the smaller inflorescence carried beneath the leaves. *Hapaline appendiculata* differs by the greatly elongated sterile spadix appendix.

The specific epithet comes from the Latin *celator* 'the concealer', in allusion to the manner in which the foliage obscures the inflorescences, a character otherwise unknown in the genus.

3. *Hapaline brownii* Hook.f., Fl. Brit. India 6: 521 (1893) & in Bot. Mag. 119, t.7325 (1893) ('*brownii*'); Ridley, Mat. fl. Malay. Penins. 3: 15 (1907) & Fl. Malay. Penins. 5: 96 (1925). Type: Malay Peninsula, Kedah, *Kunstler* (*Dr King's collector*) 1830 (holotype K; isotype BM!).

Small, tuberous, deciduous perennial herb up to 32 cm high. **Stem:** *tuber* globose, 7 – 17 × 7 – 13 mm; *stolon* terete, 1 – 4 cm × 2 – 4 mm, enclosed by several papery cataphylls. **Roots** c. 0.2 mm in diam. **Leaf:** *prophyll* linear-triangular, up to 9 cm × 5 mm, acute to apiculate; *cataphyll* linear-triangular, up to 12 cm × 9 mm, attenuate to rather blunt; *petiole* 8 – 19 cm × 0.5 – 1.5 mm; *leaf blade* cordiform, 5.5 – 16 × 2.7 – 10.5 cm, thinly coriaceous, dark green, rarely with pale green blotches, margins smooth, apex acuminate, posterior lobes rounded, ± parallel to slightly overlapping. **Inflorescence:** several together, emerging before, with or after the leaves, *peduncle* 12 – 25 cm × 0.5 – 2 mm; *spathe* 5 – 9 cm long; *spathe limb* elliptic to linear-elliptic to linear, 3 – 7 cm × 10 – 17 mm, apex acute, base decurrent into lower spathe; *lower spathe* clasping, 2 – 3 cm × 2 mm; *spadix* 5 – 8 cm × 3 – 7 mm, free portion cylindric to narrowly conic, 3 – 6 cm, tapering to somewhat blunt apically in a short appendix composed of fused synandrodes. **Flowers:** *synandria* angular-elliptic in plan view, 2 – 7 × 0.75 – 1.5 mm; *ovaries* ellipsoid, 2 – 2.5 × 0.5 – 1 mm, 2 – 4 in a single row; *stigma* slightly prominent, c. 0.2 mm in diam; *style* absent. **Infructescence:** partially enclosed by the persistent lower spathe, few-berried; *berries* ellipsoid to almost globose, c. 3 mm in diam., stigmatic remains persistent, slightly prominent. (Fig. 3.).

DISTRIBUTION. Malay Peninsula, Thailand.

MALAYSIA (PENINSULAR). Kedah: Pulau Langkawai, N side of Kisap, 30 April 1962, *Burtt & Woods* 1771 (E!, K spirit 56419!); Pulau Langkawai, Luntau (Terautau?), March 1892, *Curtis* 2819 (BM!, K!, SING!); Pulau Langkawai, *Hay* 2036 (K spirit 46306!); Kedah, no locality, May 1881, *Kunstler* (*Dr King's collector*) 1830 (holotype K; isotype BM!); Gunung Keriang, 1910, *Ridley* 14784 (SING!); Gunung Geriang, Feb. ?1910, *Ridley* 14764 (BM!, K!); Kelantan: Gua Panjang at Gua Minik, 21 Oct. 1927, *Henderson* (SING!); Batu Bow, Sungai Keteh, 10 Feb. 1924, *Nur & Foxworthy* s.n. (SING!); Gua Musang, 1 May 1976, *Stone & Sidek* 12604 (KLU!, L!); ?Penang: cult. Kew, May 1893, *Curtis* s.n., 'type' of Bot. Mag. t.7325 (K!, SING!).

THAILAND. Phuket: Tan Sang, 28 May 1919, *Haniff & Nur* 4282 (K!, SING!).

HABITAT. Disturbed mixed dipterocarp forest on river banks, on limestone, often in cracks in limestone; 20 – 150 m.

One of the collections cited above (*Burtt & Woods* 1771) is in cultivation at Edinburgh and is vigorous, with a robust spadix, large (c. 6 × 1 mm) synandria, a large spathe limb and leaves blotched pale green.

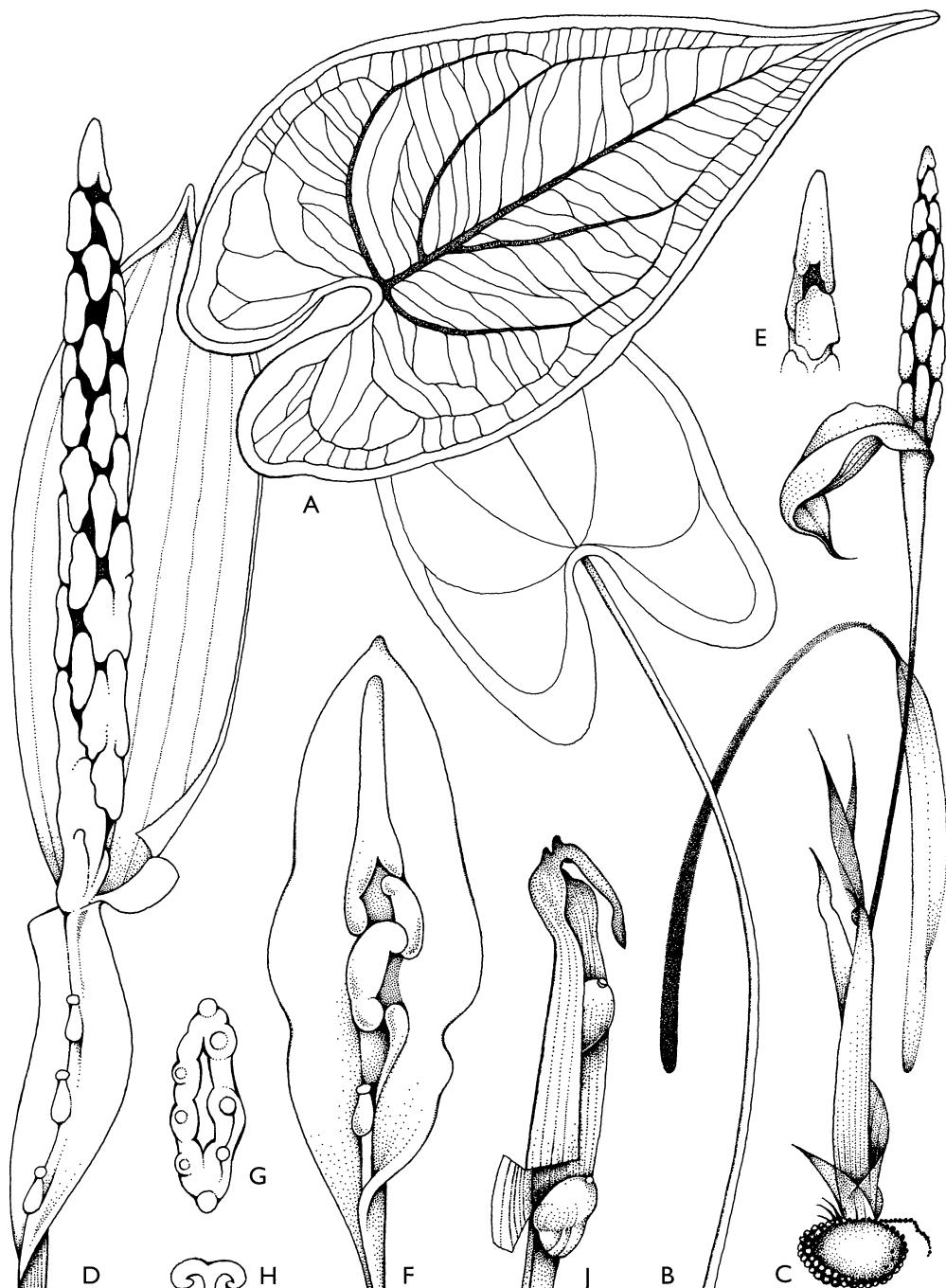


Fig. 3. *Hapaline brownii*. A — B leaf shape variation $\times 1$; C whole plant flowering $\times 1$; D inflorescence $\times 3$; E detail of spadix showing sterile appendix $\times 3$; F inflorescence $\times 3$; G synandrium, abaxial view $\times 6$; H synandrium, longitudinal section $\times 6$; J ripe infructescence $\times 2$. A — B from Kerr 4282; C, E — F from Burtt & Woods 1771; D, G — H from Hay 2036. Drawn by Emmanuel Papadopoulos.

4. *Hapaline kerrii* Gagnep. in Notul. Syst. 9: 134 (1941). Type: Thailand, Satun, Kerr 14640 (holotype K!; isotype BK!).

Slender, tuberous, deciduous perennial herb up to 30 cm high. **Stem:** *tuber* compressed globose to sub-rhizomatous, 2 – 2.4 × 1 – 1.5 cm; *rhizome* unknown. **Roots** c. 0.25 mm in diam. **Leaf:** *prophyll* broadly linear-triangular, up to 10 cm × 5 mm, acute to slightly acuminate; *cataphyll* triangular, up to 10 cm × 9 mm, acute; *petiole* 9 – 20 cm × c. 2 mm; *leaf blade* elliptic-cordiform, 5.2 – 15.5 × 2.9 – 8.5 cm, thin-textured, dark green, margins smooth, apex acute to slightly attenuate, posterior lobes overlapping. **Inflorescence:** 1 – 4 together, emerging before the leaves, occasionally with them; *peduncle* 18 – 24 cm × 1 – 2 mm; *spathe* 5 – 8.5 cm long; *spathe limb* oblong-elliptic, 3 – 6.5 × 1 – 1.1 cm, apex acute, base decurrent into lower spathe; lower spathe *spathe* margins clasping, 1 – 1.5 cm × 1 – 1.5 mm; *spadix* 4.5 – 9 cm × 1 – 2 mm, free portion cylindric, 3.5 – 5 cm, tapering apically into a short appendix composed of free synandrodies. **Flowers:** *synandria* 3 – 4 × 1 mm, oblong in plan view; *ovaries* compressed ellipsoid to bottle-shaped, 2 × 1 mm, solitary; *stigma* capitate, c. 0.33 mm in diam, *style* c. 0.5 mm long. **Infructescence:** Unknown. (Fig. 4.).

DISTRIBUTION. Thailand.

THAILAND. Chaiyaphum: Phu-Landca Forest Reserve, 1981, *Vamanonda* 3 (K spirit 4648!); Satun: Tung Nui, 17 March 1928, *Kerr* 14640 (holotype K!; isotype BK).

CULTIVATED. Cult. Bangkok, from plant brought from Saraburi without exact locality and grown in Kerr's garden, March 19 – May 22 1930, *Kerr* 19462 (K!).

HABITAT. Evergreen forest, in crevices of limestone rocks; 100 m.

Hapaline kerrii is known from only three collections and appears to be very rare in Thailand. However, it might be that it is simply overlooked in the field since the collections are quite widely scattered. The *Vamanonda* 3 collection grew well at Kew for a number of years but eventually rotted during the winter dormancy period.

Collection notes made by Mrs D.J. Collins on the *Kerr* 19462 collection state 'Perfume – musk eau de cologne.. Stem indistinct mottling of pinky grey and greyish white – sheath of stem pink'.

5. *Hapaline benthamiana* Schott, Gen. Aroid. 44, t.44 (1858); Gagnepain in Lecomte (ed.), Fl. Gén. l'Indo-Chine 6: 1131 – 1132 (1942); Hu in Dansk. Bot. Ark. 23: 426 – 427 (1968). Type: Burma, *Wallich* 1955 (holotype K!).

Hapale benthamiana Schott in Oesterr. Bot. Wochensbl. 7: 85 (1857), *in syn., nom. rejic.* (see Nicolson 1981, Eichler *et al.* 1984).

Slender, tuberous, deciduous perennial herb up to 30 cm high. **Stem:** *tuber* globose to compressed globose, 5 – 12 × 4 – 7 mm; *stolon* 2 – 6.5 cm × 2 – 3 mm, sparsely to densely clothed with numerous papery cataphylls. **Roots** c. 0.33 – 1 mm in diam. **Leaf:** *prophyll* narrowly triangular, up to 6 cm × 15 mm, acute to attenuate; *cataphyll* linear to oblong-triangular, up to 11 cm × 9 mm, acute to rounded; *petiole* 4 – 30 cm × 0.5 – 3 mm; *leaf blade* variably sagittate, lamina occasionally slightly constricted at the junction of the anterior and posterior

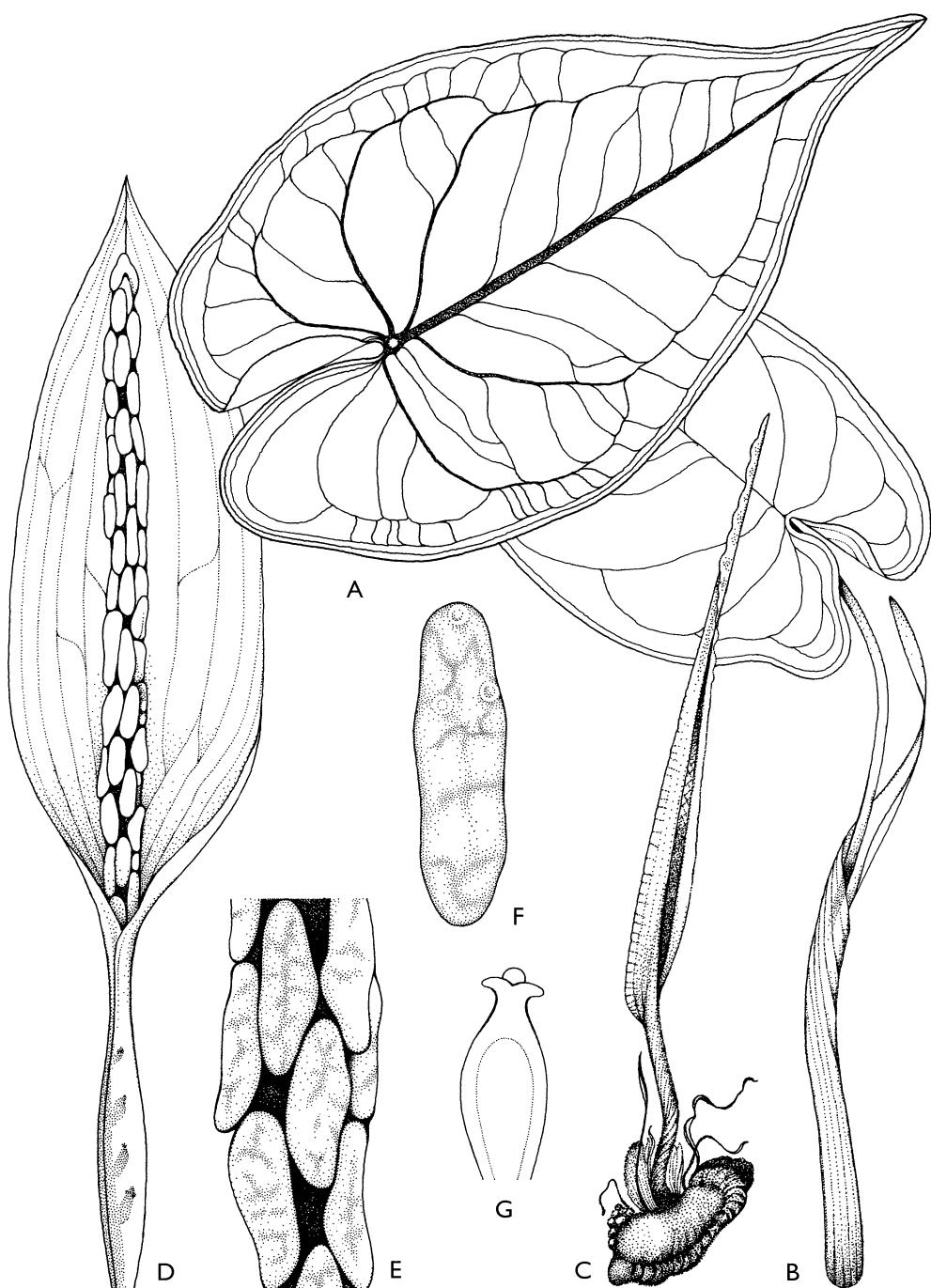


Fig. 4. *Hapaline kerrii*. A leaf $\times 2$; B vegetative shoot $\times 1$; C whole plant just beginning growth $\times 1$; D inflorescence $\times 2$; E detail of male part of spadix $\times 6$; F synandrium, plan view $\times 10$; G ovary, longitudinal section $\times 14$. Drawn from Kerr 14640 by Emmanuel Papadopoulos.

lobes, $5.5 - 17 \times 1.5 - 8.5$ cm, margins smooth to slightly crispulate, apex attenuate-acuminate to attenuate, posterior lobes subacute to slightly rounded, divergent. **Inflorescence:** emerging with or after the leaves, 1 – 3 together; *peduncle* 9 – 17 cm \times 0.5 – 1 mm; *spathe* 4 – 8.7 cm long; *spathe limb* elliptic, 2.5 – 6.5 cm \times 4 – 11 mm, apex acute, minutely apiculate, base long-decurrent into lower spathe; *lower spathe margins* clasping, 1.5 – 3.3 cm \times 2 mm; *spadix* 3 – 6 cm \times 1.5 – 1.75 mm, free portion 2.8 – 5.5 cm, cylindric, tapering apically into an appendix composed of free synandrodes. **Flowers:** *synandria* elongate-elliptic in plan view, 5 – 11 \times 1 – 1.5 mm; *ovaries* ovoid, 2 \times 1.20 mm, c. 7 in 2 staggered rows; *stigma* capitate, c. 0.33 mm in diam; *style* c. 0.5 mm long. **Infructescence:** partially to completely enclosed by the persistent lower spathe, few to several-berried; *berries* ellipsoid to subglobose, 4 – 6 mm in diam., stigmatic remains persistent, slightly prominent. (Fig. 5.).

DISTRIBUTION. Burma, Laos, Thailand, Vietnam.

BURMA. Banks of the Attran river, May 1827, Wallich 1995 (holotype K!).

LAOS. Saravan: 5 km from Khong, 1875-1877, Harmand s.n. (BM!, K!).

THAILAND. Chaiyaphum: Phu-Landca Forest Reserve, 1981, Vamanonda 2 (K spirit 46482!). Chanthaburi: Koh Chang, Klong Majum, 2 April 1959, Sørensen, Larsen & Hansen 7126a (C!); Koh Chang, Klong Majum, 2 April 1959, Sørensen, Larsen & Hansen 7128 (C!); Krat, 29 March 1925, Kerr 22 (number partially missing and incorrect, see Jacobs 1962) (K!). Chiangmai: Doi Suthep, 1 May 1929, Kerr 614 (K!); summit of Doi Muang Awn, Maxwell 93-320 (CMU!); Doi Suthep, 14 May 1958, Sørensen, Larsen & Hansen 3424 (C!); Doi Inthanon National Park, 21 July 1988, Phengklai et al. 6723 (BKF!); Doi Chiang Dao, 6 May 1956, Phloenchit 1204 (BKF 15611!); Doi Inthanon, 10 May 1959, Sørensen, Larsen & Hansen 3359 (BKF 3359!, C!, L!); Wang Tao, 20 May 1958, Sørensen, Larsen & Hansen 3548 (C!). Lampang: Ngao, 8 May 1954, Amnaj 25 (BKF 11278!). Lamphun: Doi Kuhn Dahn N.P., Mah Meun Station, 3 June 1993, Maxwell 93-533 (CMU!); Doi Kuhn Dahn N.P., trail to Mah Meun Station, 28 June 1993, Maxwell 93-719 (CMU!). Loei: Phu Kradung, 6 May 1951, Smitinand & Phloenchit 291 (BKF 5116!). Nakhon Panom, Tat Panorn, 11 May 1932, Kerr 21403 (K!, L!). Ratchaburi: Sai Yok, 1 July 1963, Larsen et al. 10378 (C!). Tak: Larn Sarng National Park, c. 17°20'N, 98°50'E, 29 May 1973, Geesink, Phanichapol & Santisuk 5515 (K!, L!).

VIETNAM. Exped. of Dr Harmand d'Indo-Chine, 1875-1877, Glaziou s.n. (BM!, K!).

CULTIVATED. Cult. Bangkok from a plant collected in Saraburi at Muak Lek, inflorescence 24 March 1919, leaves 8 June 1919, Kerr 17574 (K!); Cult. Bangkok, no further data, 5 June 1930, Kerr s.n. (K!).

HABITAT. Evergreen moist to degraded mixed deciduous forest or bamboo forest, on granitic stone or limestone; 60 – 1200 m.

Hapaline benthamiana is common throughout Thailand and extends into Burma, Laos and Vietnam. It often occurs as extensive colonies as a result of the long stolons, a feature first noted in literature by Hu (1968). Leaf shape is quite variable and intergrades to some extent with *H. brownii*. However, the thinner-textured leaves of *H. benthamiana* never have rounded, overlapping posterior lobes.

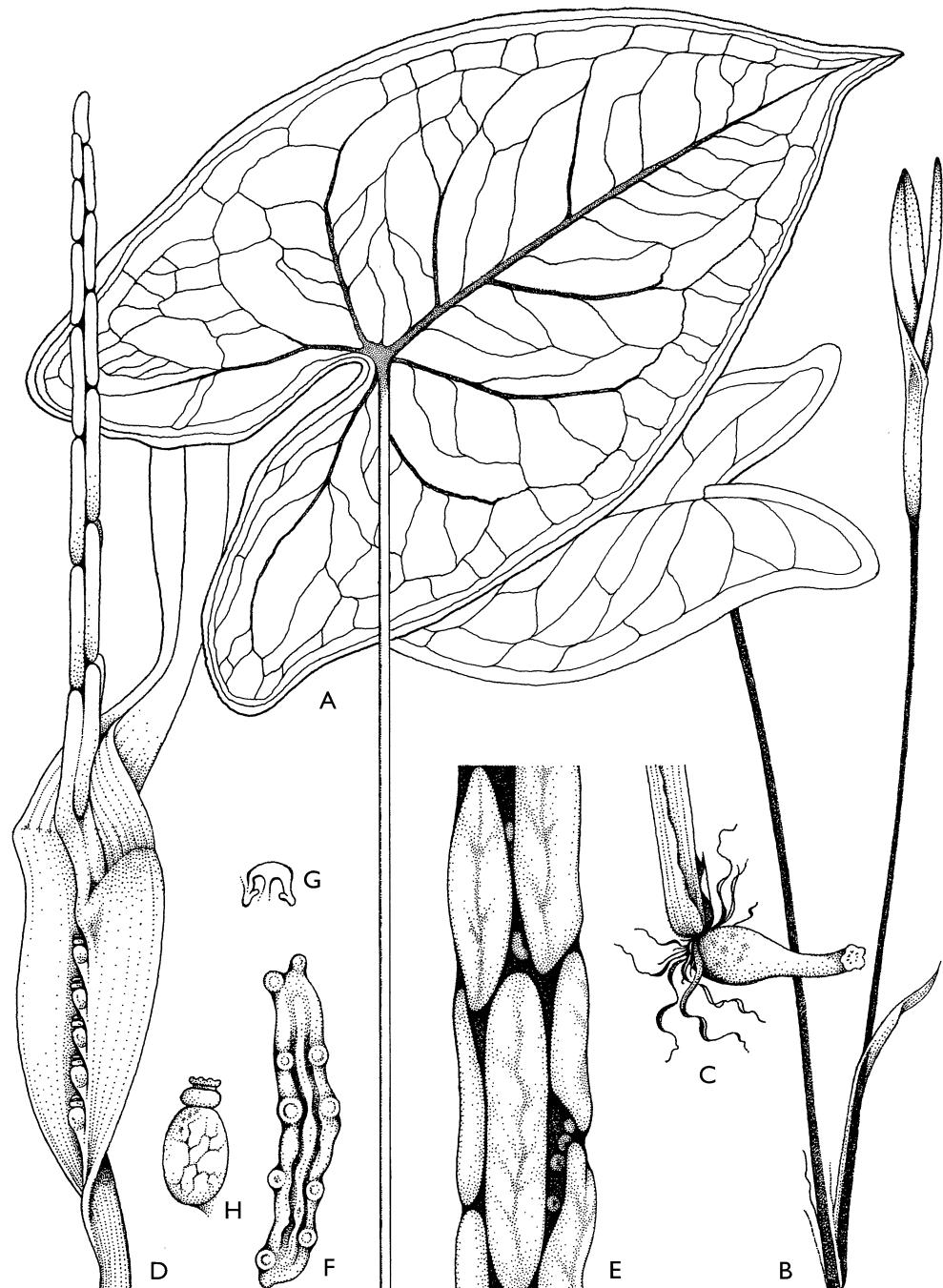


Fig. 5. *Hapaline benthamiana*. A leaf $\times 1$; B flowering shoot $\times 1$; C base of stem showing tuber and broken stolon $\times 1$; D inflorescence $\times 3$; E detail of male part of spadix $\times 10$; F synandrium, abaxial view $\times 10$; G synandrium, longitudinal section $\times 10$; H ovary, side view $\times 10$. A from Phengklai et al. 6723; B, E from Kerr s.n.; C from Stone & Sider 12604; D, F – H from Vamanonda 2. Drawn by Emmanuel Papadopoulos.

Hapaline ellipticifolia, described from China (Yunnan) but now known to occur in Burma, is probably most closely related to *H. benthamiana*. It differs by characters of leaf blade and ovary shape and by its greater stature.

Two of the collections cited (*Geesink et al.* 5515 and *Maxwell* 93-719) have leaves with pale green blotches.

6. *Hapaline ellipticifolia* C.Y. Wu & H. Li in *Acta Phytotax. Sin.* 2: 775 (1977) ('*ellipticifolium*'), Kurz in *J. Asiatic Soc. Bengal*, Pt. 2, *Nat. Hist.* 42(2): pl.9 (1873) (as *H. benthamiana*), Wu, C.Y. & Li, H. in Wu, C.Y. & Li, H. (eds), *Fl. Yunnan.* 2: 775 (1979) ('*ellipticifolium*'). Type: China, Yunnan, Hekou, Manlai, *Cai Khe-hua* 198, (holotype KUN!; isotypes K (photo!), KUN!, YNU!).

Slender, tuberous, deciduous perennial herb up to 43 cm tall. **Stem:** *tuber* compressed globose to rhizomatous, 2 – 2.4 × 1 – 1.5 cm; *stolon* unknown. **Roots** c. 0.25 mm in diam. **Leaf:** *prophyll* oblong-triangular, c. 5 cm × 4 mm, acute; *cataphyll* linear-triangular, up to 10 cm × 9 mm, acute; *petiole* 9 – 20 cm × c. 2 mm; *leaf blade* elliptic, 5.2 – 15.5 × 2.9 – 8.5, thin-textured, dark green, margins smooth, apex acute to slightly attenuate, posterior lobes parallel. **Inflorescence:** 1 – 4 together, emerging before the leaves, occasionally with them; *peduncle* 18 – 24 cm × 1 – 2 mm; *spathe* 5 – 8.5 cm long; *spathe limb* 3 – 6.5 × 1 – 1.1 cm, oblong-elliptic, apex acute with a 1 – 2 mm apicule, base decurrent into lower spathe; *lower spathe* margins clasping, 1 – 1.5 cm × 1 – 1.5 mm; *spadix* 4.5 – 9 cm × 1 – 2 mm, free portion cylindric, 3.5 – 5 cm, tapering apically into an appendix composed of free synandrodes. **Flowers:** *synandria* linear-elliptic in plan view, 3 – 4 × 1 mm; *ovaries* bottle-shaped, 2 × 1 mm, c. 8 in a single row; *stigma* capitate, c. 0.33 mm in diam; *style* very short. **Infructescence:** unknown. (Fig. 6.).

DISTRIBUTION. China (Yunnan), Burma.

CHINA. Yunnan, He Kou, Man Lai, *Cai Ke-Hua* 198 (holotype KUN!; isotypes K (photo!), KUN!, YUKU!).

BURMA. Pegu & Martaban, Karway, *Kurz* 268 (BM!, K!).

HABITAT. Unknown.

Hapaline ellipticifolia is close in appearance to *H. benthamiana* and differing in the shape of the ovary (bottle-shaped versus ovoid) and leaf blade outline (elliptic versus sagittate).

The *Kurz* 268 collection cited above (see also *Kurz* 1873: pl.9) has long been assumed to belong to *H. benthamiana*. However, the *Kurz* collection has a leaf blade with parallel posterior lobes and bottle-shaped ovaries.

7. *Hapaline colaniae* Gagnep. in *Notul. Syst.* 134 (1941) & in *Fl. Gén. l'Indo-Chine* 6: 1132 (1942). Type: Vietnam, Ha bac, *Colani* 2919 (holotype P!; isotypes K (photo!), P!, NSW, SGN!, US).

Rather robust, deciduous perennial herb up to 32 cm tall. **Stem:** *tuber* cylindric, 1 × 3 cm, rhizomatous in appearance; *stolon* unknown. **Roots** c. 0.25 mm in diam. **Leaf:** *prophyll* linear-triangular to oblong-triangular, up to 5 cm × 7 mm, acute;



Fig. 6. *Hapaline ellipticifolia*. A leaf $\times 2/3$; B whole plant flowering $\times 1/2$; C inflorescence $\times 2$; D detail of male part of spadix $\times 4$; E synandrium, plan view $\times 18$; F ovary, side view $\times 18$; G ovary, three quarter side view $\times 20$. Drawn from Cai Ke-Hua 198 by Emmanuel Papadopoulos.

cataphyll linear-triangular, up to 7.5 cm × 9 mm, acute; *petiole* 25 – 27.5 cm × 2 – 3 mm; *leaf blade* hastate, junction of anterior lobe with posterior lobes strongly constricted, 13.3 – 23.5 × 5.5 – 9.4 cm, thin-textured, dark green, heavily marked with diffuse pale green and silver-grey patches, margins smooth, apex acuminate to subacuminate, posterior lobes acute to subacuminate, strongly divergent. **Inflorescence:** 1 – several together, emerging slightly after the leaves; *peduncle* 8 – 16.5 cm × 1 – 1.5 mm; *spathe* 5 – 6 cm long; *spathe limb* oblong-elliptic, 3 – 3.5 cm × 8 – 11 mm, apex subacute to rather obtuse, minutely apiculate, base rather short-decurrent into lower spathe; *lower spathe* margins clasping to slightly erect, 1.5 – 2 × 1.5 – 2 mm; *spadix* 3 – 3.5 cm × 2 – 3 mm, free portion cylindric, 2.5 – 3 cm, tapering apically in an appendix composed of free synandrodes. **Flowers:** *synandria* oblong-elliptic in plan view, 6 – 8 × 1 – 2 mm; *ovaries* ellipsoid to bottle-shaped, 3 × 1 mm, c. 7 in a single row; *stigma* capitellate, c. 0.33 mm diam; *style* ± absent. **Infructescence:** enclosed by the persistent spathe tube, few-berried; *berries* ellipsoid, 4 – 5.5 × 3 × 4 mm, stigmatic remains persistent, prominent. (Fig. 7.).

DISTRIBUTION. Thailand, Vietnam.

THAILAND. Chaiyaphum: Phu-Landca Forest Reserve, 1981, *Vamanonda* 1 (K spirit 46483! & 57280!).

VIETNAM. Ha bac: Lang-met, May 1925, *Colani* 2919 (holotype P!; isotypes K (photo!), P!, SGN!).

HABITAT. Unknown.

This is the most distinctive species of *Hapaline*, with leaves with a prominent constriction at the junction of the anterior and posterior lobes and large inflorescences. A plant grown at Kew under *Vamanonda* 1 originated from Thailand and is the only record of the species outside Vietnam. Both the type collection and the plant grown at Kew have leaves with irregular pale green and silver-grey markings.

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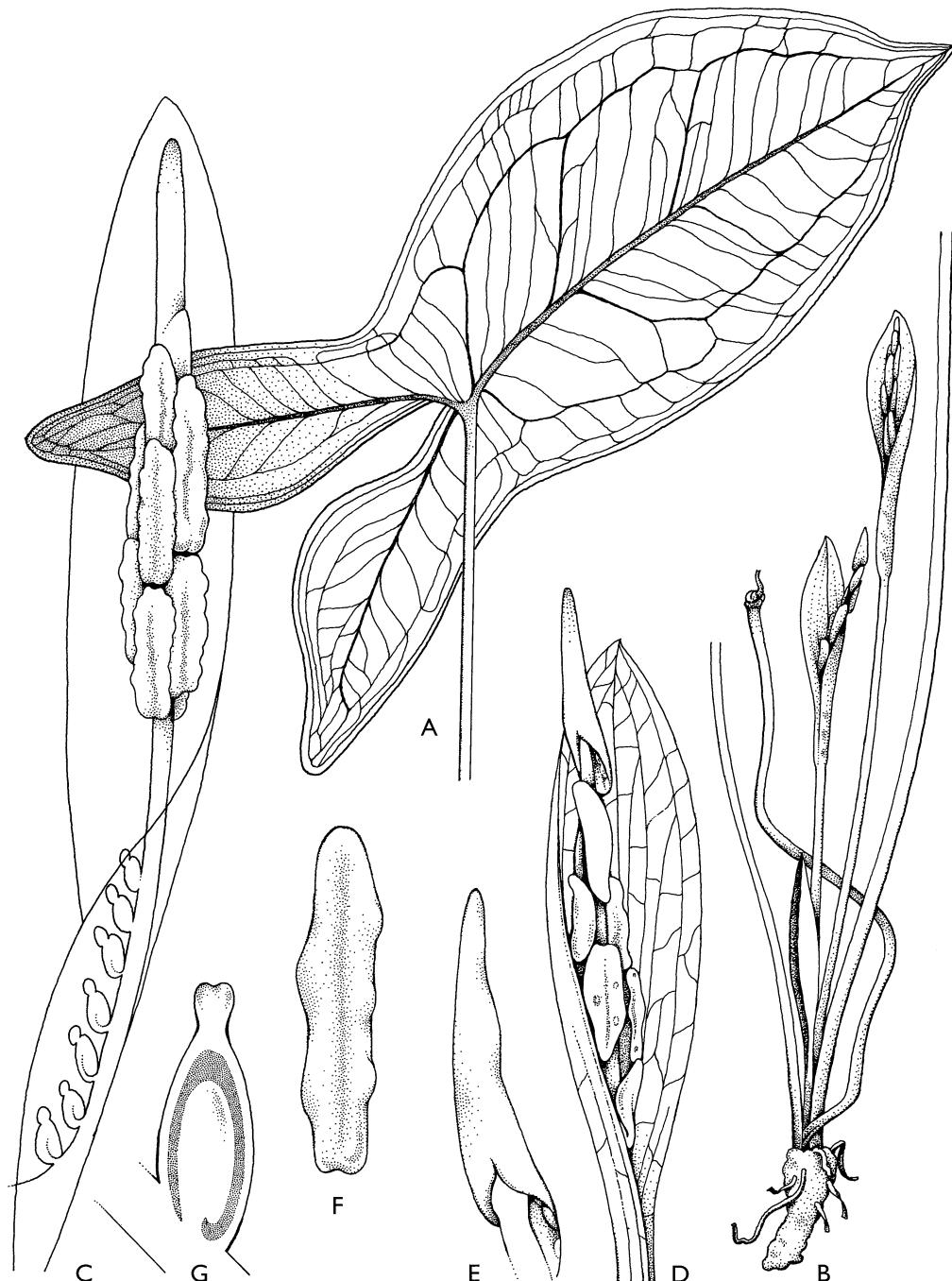


Fig. 7. *Hapaline colaniae*. A leaf $\times 2/3$; B whole plant flowering, leaves removed $\times 2/3$; C inflorescence, nearside lower spathe 'removed' $\times 3$; D inflorescence $\times 2$; detail of male part of spadix $\times 4$; E detail of sterile appendix $\times 6$; F synandrium, plan view $\times 6$; G ovary, longitudinal section $\times 14$. Drawn from Petelot 2919 by Emmanuel Papadopoulos.

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