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Original Article

Adjusting cubspecific Boundaries of the Wild Banana *Musa acuminata* Complex (Musaceae) in Thailand based on Morphological and Genetic Variations

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Abstract

Thailand, a recognized cradle of wild banana *Musa acuminata* diversity, has long been considered home to four subspecies: *siamea*, *burmannica*, *malaccensis* and *microcarpa*. However, recent extensive field surveys across the country have unveiled a more complex picture, necessitating a revision of their taxonomic classification. This study revisits the subspecific classification of *M. acuminata* in Thailand, reassessing the boundaries, descriptions, and distributions of previously reported subspecies using morphological and molecular data. Our findings reveal a distinct new subspecies, *M. acuminata* subsp. *kraburiensis*, located in the Kra Isthmus. This subspecies occupies a transitional zone between *M. acuminata* subsp. *siamea* in northern Thailand and *M. acuminata* subsp. *malaccensis* in peninsular Thailand. Notably, we also discovered a northern occurrence of the latter subspecies, suggesting a potential dispersal route along the Thailand-Myanmar mountain range. Furthermore, we document novel forms within existing subspecies, i.e., yellow bract mutants and aberration of male inflorescence architecture, in addition to a new subspecific record of subsp. *truncata* in Thailand. Conversely, neither subsp. *burmannica*, subsp. *burmannicoides* nor subsp. *microcarpa* were observed during this study. Based on our comprehensive analysis of the *M. acuminata* complex in Thailand, we advocate for maintaining subspecific rather than varietal designations. A key for identifying *M. acuminata* subspecies in Thailand based on critical diagnostic characters including leaf base shape, rachis position, and the aestivation and colour of male bracts, is presented.

Key words:

Musa acuminata, subspecies, Isthmus of Kra, *truncata*, multiple male buds, phenetics, plant morphology, yellow bract

Introduction

Musa acuminata Colla, one of the two progenitors of most pleasant seedless banana cultivars, is native to Tropical Asia. Within the species, several subspecies were described based on morphology, geographical distribution, cytology, and molecular biology (Cheesman 1948, Simmonds 1956, 1962, Perrier, 2009, Šimoníková et al., 2020, Rouard et al., 2018, Martin et al., 2023). Nowadays, nine subspecies of *M. acuminata* (*banksii*, *burmannica*, *burmannicoides*, *errans*, *malaccensis*, *microcarpa*, *siamea*, *truncata*, and *zebrina*) and three varieties (*chinensis*, *sumatrana*, and *tomentosa*) were distinguished based on morphology and geographic distribution (Perrier, 2009).

The large size and herbaceous habit of the plants make it difficult to process and deposit as dry banana specimens (Nasution 1991; Wong et al. 2001). Several attempts have been made to reveal the true identities of the subspecies. Simmonds (1956) classified the complex based on blotch colour on the pseudostem, leaf sheath waxiness, bract colour and aestivation, fertility of basal flowers, fruit shape, and number of ovules per ovary. Meanwhile, De Langhe and Devreux (1960) used bract colour, fruit pedicel, apex, and section, bunch direction and density, among other key characters, and reported one new subspecies, *burmannicoides* De Langhe & Devreux, found in India. Nasution (1991) used the hermaphrodite condition of basal flowers, shape of male buds, aestivation and colour of male bracts, shape of the free tepal of male flowers, and shape of the seed, among other morphological characters to discriminate 15 varieties of *M. acuminata* in Indonesia, including *acuminata, microcarpa* (Becc.) Nasution, and *malaccensis* (Ridl.) Nasution. Later, De Langhe et al. (2000) reported a suspicious form, which they informally called *pseudo-malaccensis*, and several other subspecific hybrids within the *M. acuminata* populations found in northern Thailand. Identities of *M. acuminata* subspp. *malaccensis* (Ridl.) N.W. Simmonds, *microcarpa* (Becc.) Simmonds, and *truncata* (Ridl.) Kiew were also the problem taxa (Häkkinen and De Langhe 2001) until Wong et al. (2001) clarified that they were genetically distinct. They emphasized the significance of ecological isolation of the subspecies that the subspp. *malaccensis* and *microcarpa* were lowland (up to 600–900 m in altitude), while the subsp. *truncata* was found in mountainous areas (usually above 900 m). In addition, subspp. *malaccensis* and *truncata* were found in mainland Malaysia while the subsp. *microcarpa* was limited in its distribution to the Island of Borneo. Molecular analyses confirmed the status of these three subspecies (Wong et al. 2001).

Thailand is located at the major biogeographical region where boundaries of two distinct floristic provinces, Indochinese and Sundaic, meet (Tougard 2001). Cheesman (1948-p.27) has mentioned in one of his historic reports on bananas that “the range of variation of the (*M. acuminata*) species in Siam (Thailand) is of great importance and much needs further study.” The area of distribution of the three subspecies including: *siamea* Simmonds, *burmannica* Simmonds, and *malaccensis* (Ridl.) N.W.Simmonds are wide-ranging dispersed from southern India to Indochina and southern China to Borneo and overlapped in Thailand i.e., along Thailand-Myanmar border, southern Thailand, and Kra Isthmus Archipelago, according to Simmonds (1960). Unfortunately, since Simmonds’ last survey in the 1950s and the De Langhe et al. report in 2000, which both emphasised the northern region, none has included a thorough investigation of *M. acuminata* from the whole of Thailand. Subspecies *burmannica, burmannicoides* and *siamea* form a complex with geographical distribution covering northeast India, Burma, southern China and Thailand and molecular cytogenetic data indicated these three subspecies should be merged to *burmannica* (Perrier, 2009, Martin et al., 2020, Martin et al., 2023). This complex is closer to subsp. *malaccensis* based on genetics than other subspecies (Perrier et al., 2011). Genome assemblies indicated hybridization between subsp. *burmannica* and subsp. *malaccensis*, which is supported by their overlap in distribution (Rouard et al., 2018, Perrier et al., 2011).

We have collected and investigated several hundreds of *M. acuminata* and related accessions throughout Thailand, in a race against time to collect and protect valuable germplasm that will increase knowledge of their variations and, hopefully, may solve the status of their taxonomic complex. Specimens were carefully

characterized, recorded, preserved and deposited in herbaria. Representatives of each taxon are cultivated as *ex situ* references. Phenetic study of morphological characters was applied along with molecular phylogenetic relation among the accessions. Dendrograms generated represent clear placement of each subspecies. We, herein, propose a new key to the subspecies of the *M. acuminata* complex in Thailand.

Materials and Methods

Taxon sampling

All specimens were collected during the years 2005–2010 on several expeditions in Thailand and identified based on previous descriptions of Cheesman (1948), Simmonds (1956, 1962), De Langhe and Devreux (1960), and De Langhe et al. (2000). A total of 211 accessions of *Musa acuminata* Colla *sensu lato* from natural habitats were studied (Table 1 Supplement). The outgroup taxa were wild *M. itinerans* Cheesman from three populations and wild *M. rubra* from seven populations. Specimens of each accession deposited at the Suan Luang Rama IX herbarium, 111 Srinakarin Road, Bang Mod, Thung Khru, Bangkok 10160, Thailand, included male inflorescence and fruits from a middle hand preserved in-spirit. In addition, the base, middle, and tip of the intact mature leaf were dried. A young curling (cigar) leaf was collected for DNA analysis. All accessions were characterised on sites using the improved banana collecting form (available in pdf file format upon request) and standard colour chart based on Descriptor for Banana (IPGRI-INIBAP/CIRAD, 1996), with essential modification using discriminating characters from Simmonds and Shepherd (1955), De Langhe and Devreux (1960), Simmonds (1962), Argent (1976), and Nasution (1991). The exact location (Figs 1) and elevation (alt.) of each accession were recorded by GPS tracker along with photographs and line drawings. The floristic regions and provinces (Changwats) of Thailand are indicated based on the system in the Flora of Thailand manuscripts (The Forest Herbarium, 1970-2023) (Table 1S)

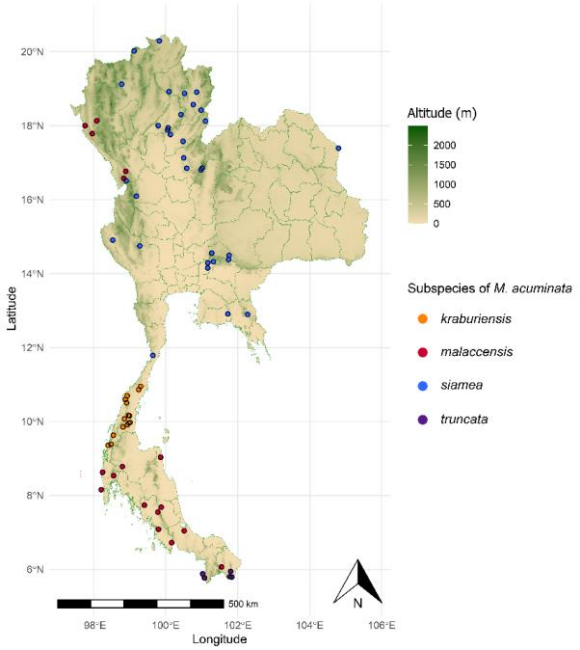

Figure 1. Collection sites of the *Musa acuminata* complex distributed in Thailand. Coloured circles indicate each taxon. The map was constructed with R studio (RStudio Team, 2020).

Morphological analysis

A total of 16 morphological characters and 195 accessions were assessed from the field. All data was transformed to numeric states in the conventional way (Table 1, Table 2S). Similarity coefficients were then analysed using Past 4.05 (Hammer et al., 2001). The characters used in the analyses were assumed to be equal and unweighted. The Unweighted Pair Group Method with Arithmetic (UPGMA) analysis using Euclidean coefficient. The discriminating characters were manually investigated from the dendrogram and mapped characters to make a key to subspecies of *M. acuminata*.

Table 1. Coding of 16 morphological characters for use in UPGMA multivariate analysis.

#	Characters	State 1	State 2	State 3	State 4	State 5	State 6
1	Petiole canal	open with margin spreading	wide with erect margins	straight with erect margins	margins curved inward	margins overlapping	
2	Leaf base	cuneate	oblique	round	cordate	auriculate	
3	Peduncle colour	green	blue				
4	Bunch direction	horizontal to angle	erect				
5	Number of rows in fruit hand	uniseriate	biseriate				
6	Rachis diameter	slender	non-slender				
7	Rachis direction	hanging vertically	at an angle	with a curve	horizontal	erect	
8	Male bud direction	vertically	downward	upward	erect		
9	Male bud number	one	numerous				
10	Bud shape	ovate	acuminate	obtuse			
11	Bract imbrication	greatly overlap	slightly overlap	non-overlap			
12	Internal bract colour	pink purple, red purple, orange red	yellow	ivory	orange		
13	External bract colour	red purple	purple red to purple brown	orange red to red	blue	orange	yellow
14	Free tepal shoulder margin	entire	incised				
15	Fruit shape	tubular	fusiform				
16	Seed surface	smooth	rough				

Molecular method

Total genomic DNA was extracted from fresh cigar leaves of 20 *Musa* accessions collected in Thailand (Table 2S) using modified hexadecyltrimethylammonium bromide (CTAB) method of Doyle and Doyle (1987). Following Fu (2022), four regions of specific chloroplast sequences including *rpl32-trnL* spacer, *matK*, *trnK-rps16* spacer and *rbcL-accD* spacer were selected. The primers were performed using Primer3 (https://primer3.ut.ee/) and BLAST in NCBI (https://www.ncbi.nlm.nih.gov/genbank/). The primer pairs were designed or modified and appear in Table 2. Genomic DNA of 20–100 ng was used in 25-µL PCR reactions with master mix i-taq (iNtRON Biotechnology, Inc.), which contained 0.5 pmol each of forward and reverse primers. The PCR conditions were as follows: initial polymerase activation at 94 °C for 5 min, 35 cycles of 94 °C for 30 s, 50–62 °C for 30 s, and 72 °C for 1 min, with a final elongation at 72 °C for 5 min. PCR product qualities were verified by 1% (w/v) agarose gel electrophoresis. The PCR products were sent to BTSeq Contiguous Sequencing Services, Celemics, Inc., Korea. All sequences were submitted to GenBank (https://www.ncbi.nlm.nih.gov/genbank/: Table 3S).

Table 2. Primers used to amplify *rpl32-trnL* spacer, *matK*, *trnK-rps16* spacer and *rbcL-accD* of Musaceae.

	Region	Primer	Sequence 5' – 3'
1	*rpl32-trnL*	rpl32-trnL-F	GGT AAY MCT TTT TGA ATG GCA GTT
2	*rpl32-trnL*	rpl32-trnL-R	CTA GGA TTT MWA GGA TGC CG
3	*matK*	matK-F	GAT ACA TAG TRC AAT ATG GT
4	*matK*	matK-R	GGT TGC TAA CTC AAY GGT AGA G
5	*trnK-rps16*	trnK-rps16-F[a]	CTC TAC CRT TGA GTT AGC AAC C
6	*trnK-rps16*	trnK-rps16-R	GCA ATT GAT GTT CGA TCC C
7	*rbcL-accD*	rbcL-accD-F[a]	GCT TCM GGK GGT ATT CAT GT
8	*rbcL-accD*	rbcL-accD-R	TGT CAA CCT CAA AAA TMW G

[a] Following Scarcelli et al. 2011.

Phylogenetic analysis

Four regions (*rpl32-trnL*, *matK*, *trnK-rps16* and *rbcL-accD*) of 20 new accessions were combined with previous data of *M. acuminata* subspecies from NCBI. Sixty-eight samples (Table 3S & 4S) were obtained and aligned with MAFFT (Katoh et al., 2002) in web: https://mafft.cbrc.jp/alignment/server/index.html and manually edited with Bioedit v7.0.5 (Hall, 1999). Four separated chloroplast regions were estimated substitution models under AIC using Jmodeltest2 on XSEDE (2.1.6) as implemented in the CIPRES web portal for Bayesian inference. The phylogenetics of different subspecies of *M. acuminata* were reconstructed using *M. itinerans* and *M. rubra* as outgroups using MrBayes 3.2.7a. The Markov Chain Monte Carlo (MCMC) was performed using independent runs with four chains, printing results every 10000 generations, saving trees every 1000 generations, for a total of two million generations (Ronquist et al. 2012). Figtree v.1.4.4 (Rambaut, 2018) was used to visualise and edit trees.

Results

Based on an extensive collection of 211 accessions from over 50 expeditions spanning 20 years, we documented a remarkable diversity of *M. acuminata* throughout Thailand, defining the geographic and altitudinal distributions of its subspecies (Figs 1 and 2). *Musa acuminata* subsp. *siamea* exhibits the broadest

distribution, occurring predominantly in the central plain and extending northward, south-eastward, and south-westward. Limited occurrences of wild *Musa* species were observed in the northeast and east, likely due to the scarcity of intact forests and natural habitats.

Musa acuminata subsp. *kraburiensis*, a newly described subspecies, discovered on mountain to lowlands and near sea beach, was restricted between 9 and 11°N latitude the area around junction between Tanao Si/Tenasserim and Phuket mountain ranges in the Kra Isthmus region (Chumphon and Ranong). In contrast, subsp. *malaccensis* was commonly found throughout peninsular Thailand. Notably, we discovered new localities of *M. acuminata* subsp. *malaccensis* in northern Thailand at elevations considerably higher (200–1000 m alt.) than previously reported for this subspecies in the south (typically below 300 m alt.). Furthermore, *M. acuminata* subsp. *truncata*, a subspecies not previously recorded in Thailand, was identified in the border region between Thailand and Malaysia around the area of Sankalakhiri/Titiwangsa mountain range (Narathiwat and Yala). In some areas, subsp. *truncata* co-occurs with subsp. *malaccensis* at lower elevations, and putative hybrids between these two subspecies were observed.

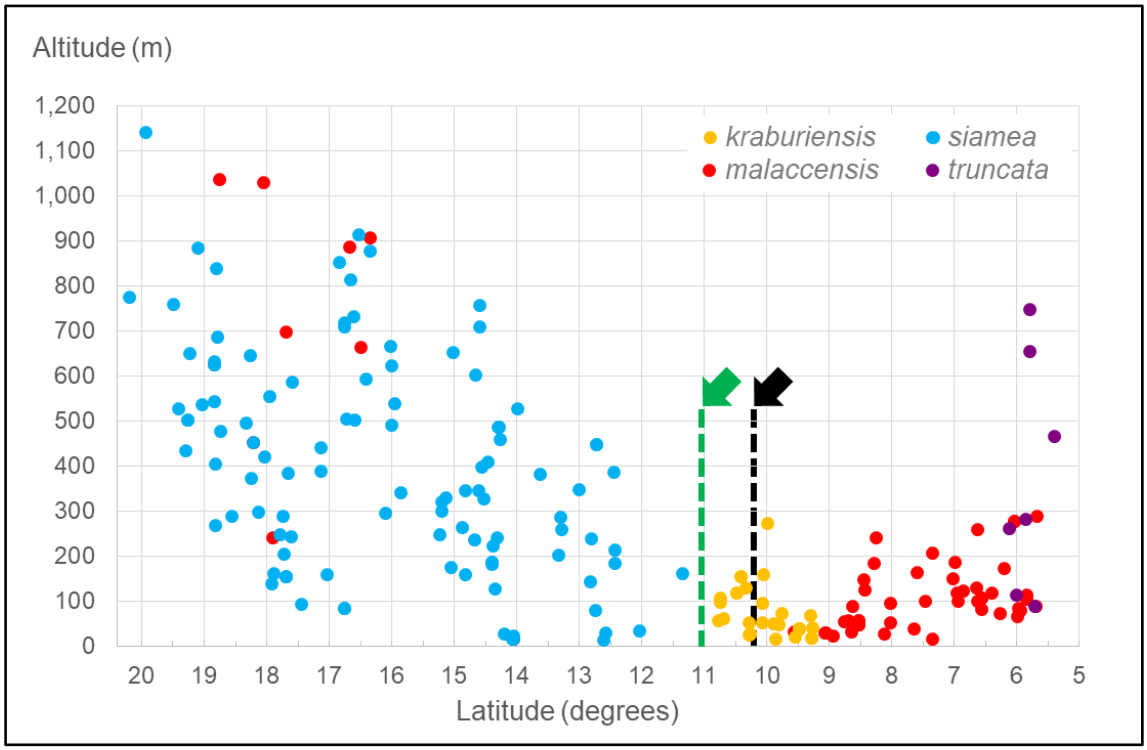

Figure 2. Distinct distribution zones based on latitudes (x-axis) and altitudes (y-axis) of *Musa acuminata* accessions of four subspecies collected in Thailand in this study. Green dash line and arrow indicated a phytogeographic transition boundary of the two subspecies, *M. acuminata* subsp. *siamea* and *M. acuminata* subsp. *kraburiensis*, just north of the Isthmus of Kra at 10–11°N latitude (black dash line and arrow).

Discriminating morphological characters

Analysis of 16 morphological characters (Table 1 & 3S) revealed several diagnostic traits for differentiating subspecies within the Thai *M. acuminata* accessions. These included vegetative characters such as leaf base shape (Figs 3), rachis position (Figs 4), and male bud shape, as well as bract colour and imbrication (Figs 5). A dendrogram generated from these morphological data (Figs 6) clustered accessions of the *M. acuminata*

complex into two major groups (Cluster I and Cluster II). These clusters were primarily distinguished by rachis position. Cluster I, corresponding to the new subsp. *kraburiensis*, exhibited a horizontal to upward-slanting or -curving rachis, while the remaining three subspecies (Cluster II) displayed a downward-oriented rachis, ranging from angled to vertically pendulous. Within Cluster II, leaf base shape, bract imbrication, and bract colour proved useful for further distinguishing subspecies. *Musa acuminata* subsp. *siamea* and/or *burmannica sensu* Simmonds was characterized by cuneate to oblique leaf bases and strongly imbricate bracts. In contrast, *M. acuminata* subsp. *malaccensis*, and *truncata* were readily distinguished by their round, cordate to auriculate leaf bases and less than 1 cm of bract apex overlap (ranging from slightly imbricate to non-imbricate). Bract colour was particularly informative, as each of the three subspecies within Cluster II exhibited a distinct coloration (Figs 5).

Musa acuminata subsp. *truncata* is markedly different from sympatric subsp. *malaccensis* by its unique bract coloration: dark purple externally and ivory internally (sometimes fading from pale red), whereas subsp. *malaccensis* exhibits red, purplish-red, or pinkish-purple bracts both externally and internally (Figs 5).

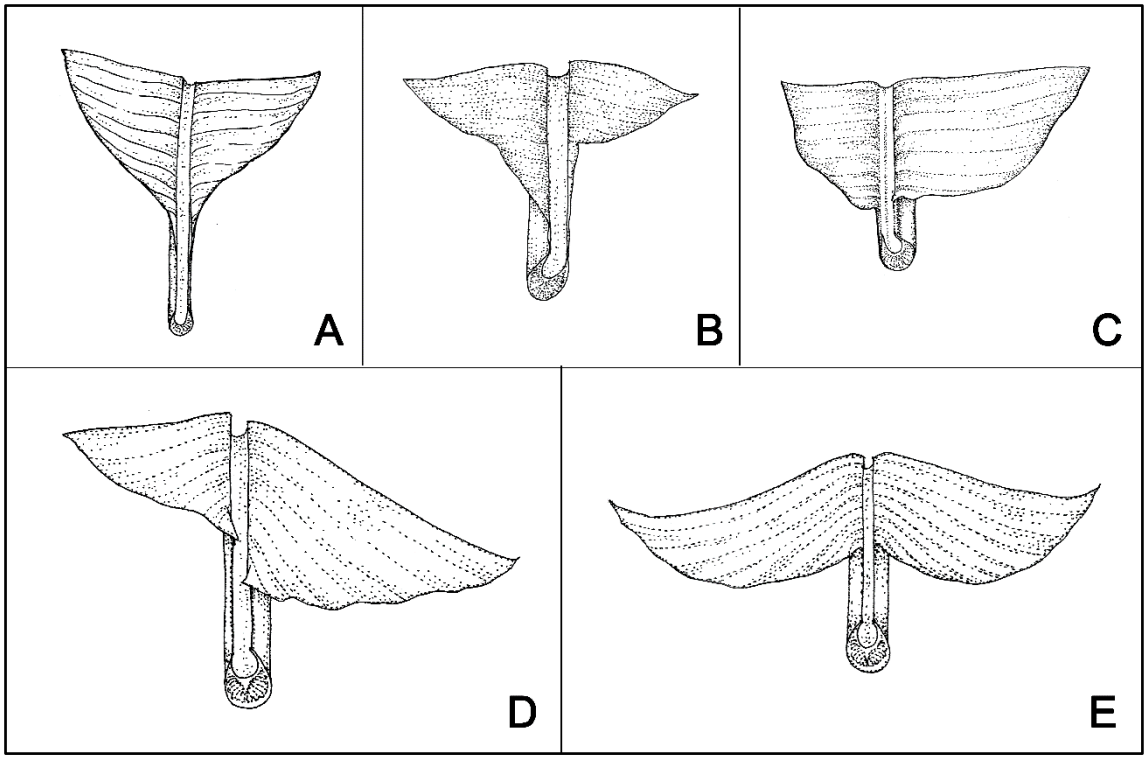

Figure 3. Variation of leaf bases found in the *M. acuminata* complex in Thailand. (A) cuneate - subsp. *siamea*, SS&JS 091, 182, 262; (B) oblique - subsp. *siamea*, SS&JS 021, 247, 266; (C) round - subsp. *kraburiensis*, SS&JS 107, 108, 142; *malaccensis,* SS&JS 204, 274; *truncata,* SS&JS 206, 490, 497; (D) auriculate - subsp. *kraburiensis*, SS&JS 009; *malaccensis,* SS&JS 005, 006, 010; (E) cordate - subsp. *malaccensis*, SS&JS 082, 138, 546. Illustrations by Potjana Kaittiprapai.

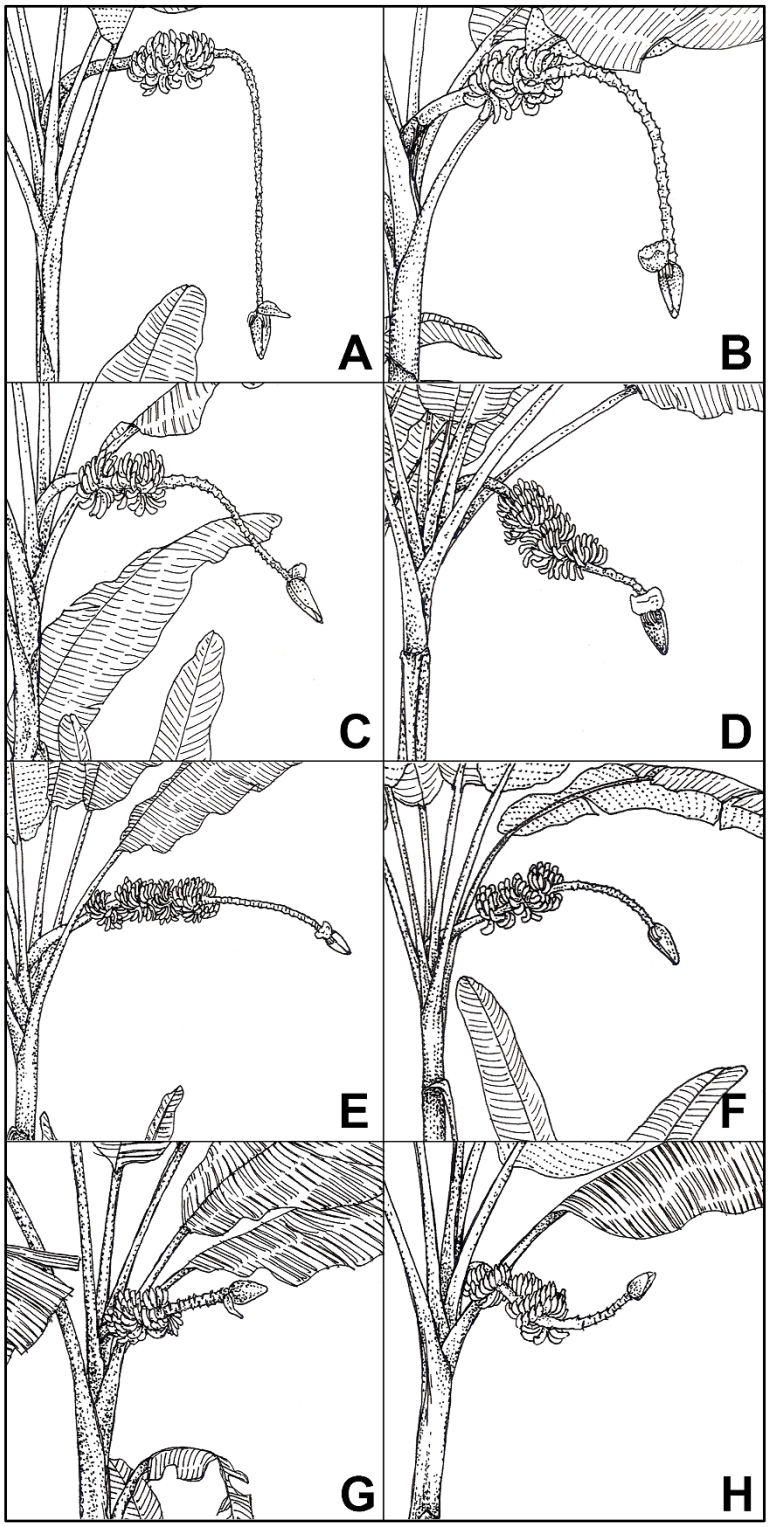

Fig. 4. Variation of rachis positions found in the *Musa acuminata* complex in Thailand. (A–B) falling vertically – subsp. *siamea*, SS&JS 172, 007; (C) at an angle downward – subsp. *siamea*, SS&JS 247; (D) downward with a curve – subsp. *truncata* 206; (E–F) horizontal to sub horizontal – subsp. *malaccensis* (typical form) – SS&JS 204, 203; (G) horizontal to slanting upward – subsp. *kraburiensis*, SS&JS 104; and (H) curving upward – subsp. *kraburiensis*, SS&JS 107. Illustrations by Potjana Kaittiprapai.

Figure 5. Male buds of *Musa acuminata* subspecies in Thailand showing variation of shapes, aestivation, and colours of buds; (A–C) subsp. *kraburiensis* - SS&JS 108, 107, 142; (D–F) subsp. *malaccensis* - SS&JS 140, 485, 138; (G–I) subsp. *siamea* - SS&JS 021, 091, 266; (J–K) subsp. *truncata* - SS&JS 491, 497 and (L) comparison of spp. *truncata* - SS&JS 206 and *malaccensis* nearby (no collection). The pictures were arranged by natural orientations of the male buds and not to scale. Photos by S.C.S.

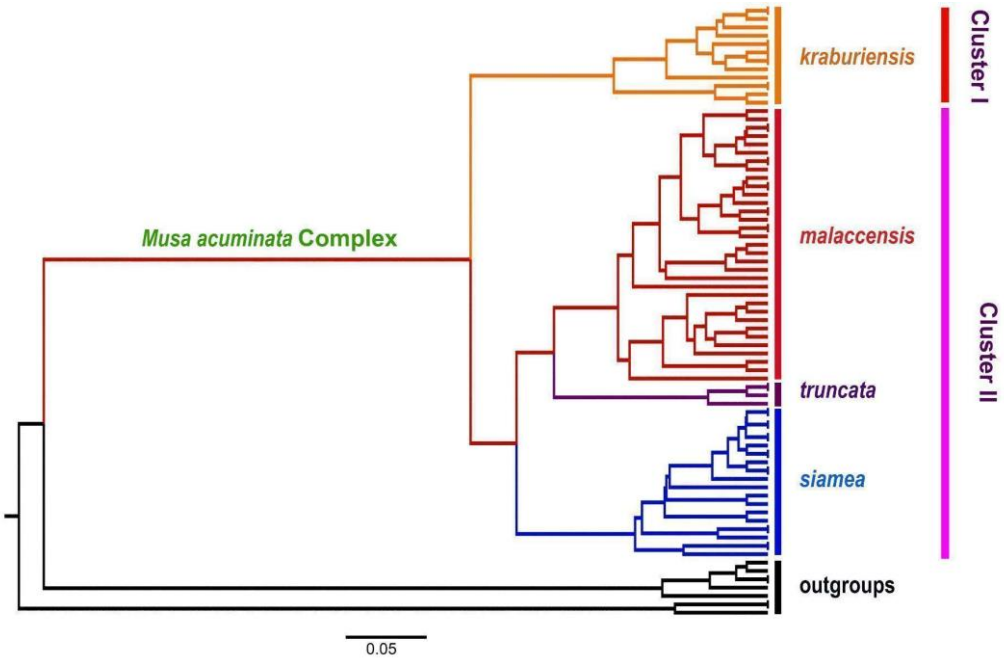

Figure 6. Dendrogram of 195 accessions of *Musa acuminata* and six outgroup species obtained with the UPGMA clustering algorithm based on 16 morphological characters.

Morphological Aberrations in *Musa acuminata subspecies*

In addition to the known variation in leaf base shape, rachis position, aestivation, and male bracts in *M. acuminata* complex, we revealed unusual bract colour and inflorescence morphology anomalies in natural Thai populations. These included yellow bract mutants in *M. acuminata* subspp. *siamea* and *kraburiensis* and curious alterations in inflorescence architecture in *M. acuminata* subsp. *siamea*.

Recently, the new form *byssina* (Figs 7A–B) of *M. acuminata* subsp. *siamea* has been discovered among their typical red purple inflorescence clans in several locations in Chanthaburi (SE Thailand), Nakhon Ratchasima (E Thailand) and Kamphaeng Phet (N Thailand). Meanwhile, in Ranong (Peninsular Thailand), a yellow bract mutant population of *M. acuminata* subsp. *kraburiensis*, named f. *luteola* (Figs 7C), was observed sympatrically alongside the normally red-purple individuals. This latter form of around 50 clumps scatters in an open hillside area of approximately 4 square kilometres. Animal visitation was observed in both the mutant and wild-type forms (Nilapaka's pers. obs.). The yellow bract mutant was reported to be deprived or absent of flavonols and anthocyanins with suspecting in mutations of either flavonol synthase, dihydroflavonol reductase or some other related genes in these pathways (Kitdamrongsont et al. 2008 and Pothavorn et al. 2010). The occurrence of yellow bract mutants is high in some areas. This might be from population stratification and inbreeding within small patches of population in the areas due to deforestation.

The present study also reported anomalies in the inflorescence architecture in a clone of *M. acuminata* subsp. *siamea*. This mutant form, f. *nanakornii* (Figs 7D, Figs 8, Figs 11), has been cultivated by the several Hmong hill-tribe communities living on the highlands in N and NE Thailand. Its Thai name, 'Roi Pli,' explains the occurrence of numerous male buds developing on the main inflorescence rachis. Each male flower on the hand differentiates into a male inflorescence, sometimes with extended rachilla, causing the inflorescence to look like a chandelier. Note that while this forma typically does not produce seeded fruit, an accession bearing fruits with a few seeds has been found.

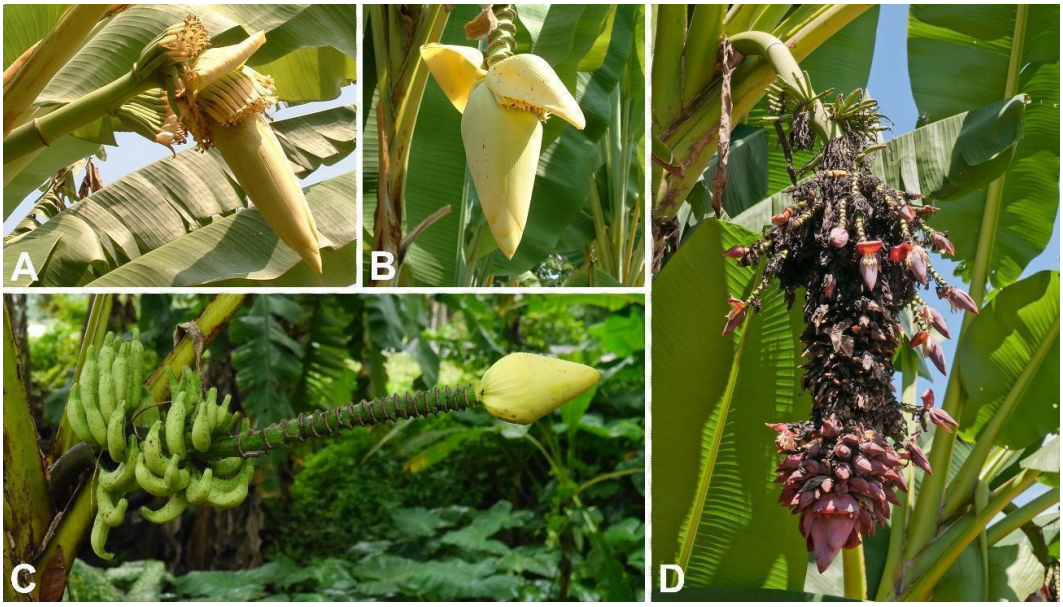

Figure 7. Morphological aberrations in *Musa acuminata* subspecies; (A–B) female and male inflorescences, respectively, of a yellow bract mutant *M. acuminata* subsp. *siamea* f. *byssina* Swangpol & Athawongsa, form. nov., SS&JS 173, from Nakhon Ratchasima (NE Thailand); (C) male inflorescence of a yellow bract mutant *M. acuminata* subsp. *kraburiensis* f. *luteola*, Swangpol & W.Inta, form. nov., SS&JS 251, from Ranong (Peninsular Thailand); and (D) *M. acuminata* subsp. *siamea* f. *nanakornii*, Swangpol, Chom. & Sukkaew., form. nov., with male inflorescence abnormalities, SS&JS 448 from Nan (N Thailand). Photos by S.C.S.

Figure 8. Various inflorescence abnormalities found in *Musa acuminata* subsp. *siamea* f. *nanakornii*, ordering left to right from hands of female flowers at the base of the inflorescence, in the top row, to hands in each inflorescence bracts, at the inflorescence terminal, in the fourth row. Flowers in some hands, e.g., the last three ones in the 2nd row, are aborted. This specific specimen grown in Ratchaburi, W Thailand, lacks an extended rachilla. Photos by S.C.S.

Phylogenetic analysis

Phylogenetic analysis of four chloroplast regions (*rpl32-trnL*, *matK*, *trnK-rps16* and *rbcL-accD*) using maximum likelihood (ML) methods (Figs 9) resolved Musaceae as distinct from other families within Zingiberales. Within Musaceae, *Musa* formed a monophyletic group, comprising two clades corresponding to sections *Callimusa* and *Musa*. *Musa rubra* clustered with *M. acuminata*, separate from other species within *Musa*. However, these chloroplast markers did not resolve the ten previously recognized subspecies of *M. acuminata*.

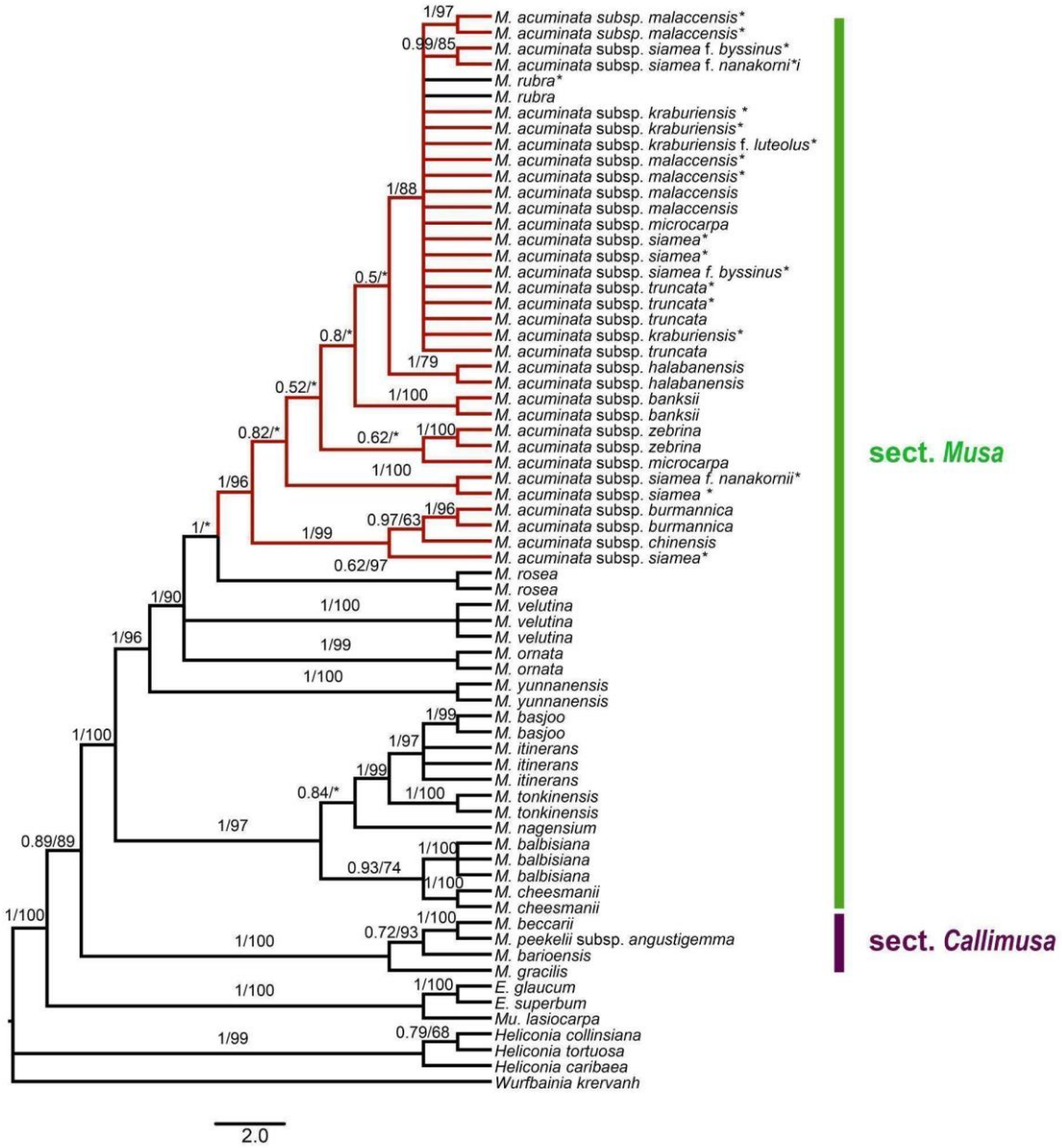

Figure 9. ML trees based on *rpl32-trnL*, *matK*, *trnK-rps16* and *rbcL-accD* showing the genetic relationships among 33 OTUs in the *Musa acuminata* complex and 35 outgroup species. Asterisk * indicated accessions from our study. List of analysed sequences appear in Table 2S.

Discussion

Previous studies investigating genetic diversity within the *M. acuminata* complex have suggested a link to geographic distribution (Cheesman 1947 and 1948; Simmonds 1956; De Langhe et al. 2000; Perrier, 2009; Perrier et al., 2011, Jenny et al. 2024). However, species delimitation within the wild *Musa* has been problematic. Herbarium specimens are often incomplete or inadequate (e.g., Simmonds 1956 and De Langhe et al. 2000), and the large, herbaceous growth habit of the bananas makes specimen preservation challenging. Furthermore, many specimens include immature fruits, which can be misleading for identification. Existing reports frequently provide limited descriptions and photographs, often focusing solely on pseudostem and inflorescence characters, which are insufficient for robust taxonomic conclusions. To address these limitations, our study emphasized meticulous field collection of fresh, dried, and spirit-preserved specimens. Crucially, we documented a comprehensive suite of morphological characters *in situ* and associated all specimens with GPS coordinates, detailed drawings and photographs incorporating a standard colour chart (IPGRI-INIBAP/CIRAD 1996) designations.

Taxonomic Status of the *M. acuminata* Complex

Segregation of the *M. acuminata* complex in Thailand into species and subspecies corroborated previous taxonomic treatments (Simmonds 1956; De Langhe et al. 2000; Wong et al. 2001; Perrier, 2009; Rouard et al., 2018). Dendrograms generated from morphological and distribution data (Figure 6) strongly supported the recognition of *M. acuminata* as a distinct species, consistent with conventional classifications (Cheesman 1948; Simmonds 1956; Nasution 1991; Wong et al. 2001; Inta et al., 2022). While ITS and chloroplast sequence data clustered *M. acuminata* with *M. rubra*, these two species were readily differentiated morphologically. Our extensive sampling of *M. acuminata* across Thailand provides substantial evidence supporting the use of subspecific ranks within the complex, a view contrasting with Nasution's classification (1991) of all *M. acuminata* variations in Indonesia as varieties. He classified 15 varieties, including nine new combinations encompassing *acuminata, malaccensis,* and *microcarpa*, but did not provide justification for these designations. Our findings align more closely with Simmonds (1956; p. 469) assertion that the various forms of *M. acuminata* represent "distinct geographico-morphological units." Indeed, the geographically defined distributions of the *M. acuminata* infraspecific taxa observed in this study are congruent with results from molecular phylogenetic analyses (Perrier, 2009).

Moreover, the status of the four subspecies: *siamea, malaccensis*, *truncata* and the newly described *kraburiensis*, are well maintained based on the morphological and sequence analyses (Fig. 6 and 8, respectively). The separation of the four subspecies, as shown in the following key, was mainly determined by leaf base shape, rachis positions, bud imbrication and the colour of male bracts. Meanwhile, several characters previously used by banana researchers were found to be highly variable among different populations within the subspecies. These ambiguous characters included blotches on the leaves of young suckers, pseudostem pigmentation, and waxiness of leaf sheaths. Also, the shape of the free tepal used by Nasution (1991) to discriminate var. *malaccensis* and *microcarpa* were not helpful. He described var. *malaccensis* as having round and acuminate free tepal and that of *microcarpa* was obovate and acute. While our previous work (Inta et al., 2022) examined floral morphological evolution in *Musa* and suggested that tepal morphology is uniform across *M. acuminata* subspecies, with all of which tepals exhibiting an elliptic shape and acuminate apex.

Indiscrimination Between Subspecies *siamea* and *burmannica*

Although *M. acuminata* subsp. *siamea* and *burmannica* (mentioned as 'Annam' and 'Tavoy' forms, respectively, by Cheesman 1948) were traditionally described as having similar obtuse, imbricate, and red-purple male buds, they were previously separated based on waxiness and pigmentation of the pseudostems, bud shapes, bunch position and compactness, and length of the fruit pedicel and apex (Cheesman 1948; Simmonds 1956; De Langhe and Devreux 1960). Our collection lacked accessions exhibiting the complete suite of Simmonds' subsp. *siamea* characteristic traits (waxy pseudostem, sub-horizontal and compact bunch, tepals often with yellow tips, and polygonal-round fruit cross-section) and Simmonds' subsp. *burmannica* which exhibits its corresponding suite of traits (non-waxy pseudostem, pendant and lax bunch, and angular fruit cross-section).

Further confusion arises from the use of fruit pedicel and apex lengths, which different authors have ascribed to the subspecies. Cheesman (1948; p. 27) described the "Tavoy form" (*M. acuminata* subsp. *burmannica sensu* Simmonds) as having "the pedicel very short and not very distinct, acumen about 0.5 cm long." Conversely, he described the "Annam form" (*M. acuminata* subsp. *siamea sensu* Simmonds) as having "a short (0.5 cm) but quite distinct pedicel and well-marked acumen 0.5 cm long". However, De Langhe and Devreux (1960) presented contrasting data in their comparative morphological table. They stated that subsp. *burmannica* has a long fruit pedicel (1 cm) and the apex (1 cm or longer), while the subsp. *siamea* has a shorter fruit pedicel and apex (0.5 cm).

Jenny et al. (2024) also reported that the morphological traits they examined were insufficient to definitively classify specimens within the subsp. *siamea/burmannica* complex, due to the morphological similarity of these specimens.

Cheesman 1948, Simmonds (1962) and Perrier (2009) reported that the subspecies *burmannica* and *siamea* distributed in overlapping areas from Southeast India and Myanmar to Vietnam. In these cases, we suspect that the banana collections reported were too limited to be definitive. Cheesman (1948, p. 22) himself noted observing only "dozen clones" of *M. acuminata* in the I.C.T.A. collection. Therefore, despite our extensive surveys along the Thailand-Myanmar border from Mae Hong Son through to Prachuap Khiri Khan, no "true" *burmannica* accession as of Simmonds was found and we cannot maintain subsp. *burmannica* in the traditional sense. We argued that subsp. *burmannica* should be included with subsp. *siamea*, possesses cuneate/oblique leaf bases and purple, red-purple to purple brown male buds with various degrees of aestivation and more than 1-cm overlapping of bract apex.

Our argument is supported by the results of the diversity array technology (DArT), simple sequence repeat (SSR) markers, molecular cytogenetics and GBS (Genotyping By Sequencing) technique which indicated that the two subspecies were not separated (Dupouy et al., 2019; Jenny et al. 2024).

According to botanical nomenclature rules (Turland, 2018), among the two subspecies proposed by Simmonds (1956), '*siamea*' takes precedence because it appeared earlier (page 466). Therefore, '*siamea*' is the accepted name, with '*burmannica*' (page 468) becoming its synonym.

M. acuminata complex of subsp. *microcarpa* and subsp. *truncata*

From its counterpart, Simmonds (1956) distinguished subsp. *microcarpa* "by the yellowish tinge and virtual waxlessness of the foliage, by the intense chocolate brown pigmentation of sheaths and, often, midribs, by the fading purple flush on the peduncle and male rachis, by the plump non-imbricate male bud, by the bracts purple without and pale red within and but weakly rolled at the time of falling and by its essentially montane distribution. The fruits are variable in size." All these morphological features, especially the male bud features (Figure 5), present variably in the subspecies *truncata, malaccensis* and *siamea* found in Thailand and could not be used for identification.

Simmonds (1956) reduced *M. truncata* to the synonym of *M. acuminata* subsp. *microcarpa* due to their similar morphology. However, AFLP and RFLP marker analyses (Wong et al., 2001 and Carreel et al. 1994; Perrier, 2009, respectively) recently revealed their distinctive status. Previous literature stated that subsp. *microcarpa* was endemic to the lowlands in the Island of Borneo (Nasution 1991; Wong et al. 2001) and subsp. *truncata* distributes in the highlands of Peninsular Malaysia (Carreel et al. 1994, Perrier, 2009). The fact that we could not find subsp. *microcarpa*, by Simmonds' description, in Thailand agrees with its geographic distribution and genome assemblies reported recently by Perrier et al. (2011) and Rouard et al. (2018). Also mentioned by Cheesman (1948) that subsp. *truncata* plants were not vigorous under the less humid and lowland conditions and all ultimately died. We suspected that the geographic isolation may have caused subspecific polymorphisms between the two subspecies.

M. acuminata Subspecies Distribution Boundaries

Our survey results confirmed Simmonds' (1956) view that Peninsula Thailand and the Thailand-Myanmar border are areas of "extreme complexity" of *M. acuminata*. *Musa acuminata* subsp. *truncata*, as a new record in Thailand, extends its natural dispersal in mountainous areas of mainland Malaysia across the Thailand-Malaysia border. We agree with earlier reports (Cheesman 1948; Simmonds 1956; Wong et al. 2001) that subsp. *truncata* is montane and did not thrive well at low altitude as we have not succeeded in maintaining the sole accession of this subspecies in our nursery near Bangkok.

Musa acuminata subsp. *siamea* is more drought and heat tolerant with the most wide-spread of all the subspecies. It was found throughout the north, central, west, northeast to the east of Thailand where 3 to 6 months of dry season is present. Evidence from other reports indicate that this subspecies has also been observed in southern China, Laos and Vietnam (Wu and Kress 2000; Lheureux et al. 2007; Jenny et al. 2024). Missing of *M. acuminata* specimens from most of the northeast and east of Thailand (Figure 1) may be due to heavy and continuity of deforestation occurring in the regions. Meanwhile, subsp. *microcarpa*, which has not been found in Thailand, probably limits its distribution to only in the island of Borneo (Perrier et al. 2011; Rouard et al. 2018). However, the real survey of subsp. *microcarpa* in the wild is needed to confirm the real existence or to be the synonym of subsp. *siamea.*

From our investigations, the area of distribution of *M. acuminata* subsp. *malaccensis* has been extended from southern Peninsula Malaysia to north-western Thailand. This subspecies prefers cool and continuous precipitation all year round. Our morphology and molecular analysis did not support the assumption of De Langhe et al. (2000) that these upper northern populations were '*pseudo-malaccensis*.' In contrast, we believed that they are typical as of their southern counterparts and hypothesised that this subspecies might have distributed along the mountain chain that had the same climate pattern from the south to the north since the ancient time when the climate was colder and had higher rainfall. When the climate was warmer and drier, the distribution range receded. Some populations have persisted in separated areas where the climate has remained wet and cool. Exploration along the rainward side of Tanao Si/Tenasserim mountain chain in Myanmar would be important to provide more evidence for this hypothesis. Subspecies *malaccensis* was commonly found in the lowlands of Southern Thailand and also growing overlapping with the population of subsp. *truncata* in the highlands of Narathiwat and Yala. The fact that they were found at approx. 200–1,000 m above sea level in northern Thailand, lead us to conclude that it has a much wider altitudinal range than has previously been reported (Ridley 1924, Simmonds 1956, Wong et al. 2001, Nasution, 1991, Perrier, 2009).

Aberration of *M. acuminata* subspecific Forms

Three new derivations of *M. acuminata* subspecies are reported in this manuscript (Figure 7): two forms with yellow bracts and one with intriguing inflorescence morphology. Many *Musa* taxa have been listed having yellow bracts, e.g., *M. basjoo* Siebold ex Miq. (Miquel 1867), *M. siamensis* Häkkinen & Rich.H.Wallace (Häkkinen and Wallace 2007) and *M. acuminata* var. *flava* (Ridl.) Nasution (Nasution 1991). The two newly described forms, f. *byssina* and *luteola* clearly belong to *M. acuminata* subspp. *siamea* and *kraburiensis*, respectively. They can be differentiated from *M. acuminata* var. *flava* because this native variety of Kalimantan and Malay Peninsula possesses the feature suite of cuneate/oblique leaf base and convolute male bud. The forma *byssina* is named for its bracts of light yellow, similar to the colour of raw silk and *luteola* means golden-yellow or the colour of egg yolk (Eckel 2010–2023).

In their natural habitats, f. *byssina* was found to be less common than f. *luteola*. It is not really less common. The area around south of Phanom Dongrek mountain has many yellow bract populations but is patchy distributed in large areas and can grow only where it has enough moisture and less human disturbances. Despite being observed in only one area of the Kra Isthmus, f. *luteola*'s population spread over 4 km, and the clump number reached a number of up to 50. In contrast, f. *byssina* was represented by only a single clump in each of several locations among typical red-purple *M. acuminata* populations. Nevertheless, preliminary observations showed squirrels and bats visiting the yellow flowers of the f. *luteola* at night, and insects visiting by day. (W. Nilapaka pers. obs.). The lighter bract colour may attract these nocturnal and diurnal visitors. Bract colour may not be crucial for pollinator attraction. Smell or nectar and pollen contents are more crucial.

The extraordinary inflorescence architecture of *M. acuminata* subsp. *siamea* f. *nanakornii* (Fig. 7D) has attracted plant enthusiasts and researchers alike. Due to infertility of the form, the three initially specimens collected were vegetatively propagated and grown by the villagers as an ornamental plant. Academically, a clone found in Chiang Mai has been introduced into the Queen Sirikit Botanic Garden and Chomchalow et al. reported these bunch mutational occurrences for the first time in 2014. The aberration with a male inflorescence replacing each flower on the hands of the banana bunch is possibly caused by abnormalities involving flower and inflorescence meristem indeterminacy. This mutation might involve an abnormal expression of a transcription factor or some genes in related pathways. The genetic and hormonal regulations of the inflorescence meristem activity have been reviewed in angiosperms (Thompson and Hake 2009) and studied in monocots e.g., corn (Laudencia-Chingcuanco & Hake 2002; Chuck, Meeley & Hake S 2008; Chaudhry, Chen & Gallavotti 2024) and grass (Bommert & Whipple 2018) and dicots e.g., cauliflowers (Azpeitia et al 2021). However, a lot of studies about genome, transcriptome and cell/tissue differentiations are required since there is almost no study about inflorescence formation in bananas before.

There are five main conclusions from this study. Firstly *M. acuminata* is a good species whose variation is discontinuous from the other related species investigated. Secondly, the use of subspecific rank within the *M. acuminata* complex is considered the most suitable way of dealing with the variation encountered from our wide-ranging collections of bananas throughout Thailand. Thirdly, subsp. *microcarpa* has not been found in Thailand and subsp. *burmannica* cannot be maintained and is reduced to synonymy with subsp. *siamea*. Fourthly, the addition of subsp. *kraburiensis* as a newly described subspecies and subsp. *truncata* as a new record to the Thai flora brings the total number of the Thai subspecies to four. Lastly, the taxonomic status of these four *M. acuminata* subspecies: *kraburiensis*, *malaccensis*, *siamea* and *truncata* found in Thailand are supported by morphology.
Compiling from this study, besides geographic distribution, the most important morphological characters for the determination of these *M. acuminata* subspecies are: leaf base shape, rachis position, male bract imbrication and colour of bracts. The minimal collection requirements for accurate identification are: the base of one mature leaf, a male bud, and a hand of fully mature fruits. In addition, four series of photographs are needed: (1) the clump of pseudostems with a mature bunch showing the rachis position; (2) leaf base and apex on their adaxial side and middle part of the leaf on its abaxial side to represent waxiness and colour of the

underside; (3) the male bud and outermost bracts showing their shapes, external and internal bract colours, and reflexing after anthesis; (4) the male flowers showing the adaxial side of the compound tepal, free tepal, stamens and pistil. The standard colour chart (e.g., IPGRI-INIBAP/CIRAD 1996) and a scale should always accompany all photographs.

For further study of genetic variations, mixing among each subspecies and actual natural distribution of subpopulations in *M. acuminata* along with geographic locations, multi-genetic loci assay such as SSR, SNPs or inter-MITE are required.

Taxonomic treatment

Musa acuminata Colla, Mem. Gen. Musa 25: 394. 1820, lectotype (designated Hakkinen & Vare 2008); Cheesman, Kew Bull. 3: 17–28. 1948 (1949); U.O.P.Z.: 359 (photo. opp.), 373 (1949); Simmonds & Shepherd, Nature 169: 507–508. 1952; Simmonds, Kew Bull. 14, 2: 198–204. 1960; Zollinger, Syst. Verz. Ind. Archip. 74. 1854; Kurz, Journ. Agric. Hort. Soc. India n.s. 5: 112–168. 1878 p.p.; Baker, Ann. Bot. 7, 26: 215. 18943 excl. var. culta Kurz et syn. Berterii Colla et aphurica Rumph. — *Musa simiarum* Miq. Fl. Ind. Bat. 3: 589. 1855; Kurz, Journ. Agric. Hort. Soc. India 14: 297. 1867. — *Musa zebrina* Van Houtte ex Planch., Flore des Serres 10: 223 et t. 1061–62. 1855; Backer, Flora van Java 3: 136. 1924. — *Musa malaccensis* Ridl., Trans. Linn. Soc. Ser. 2, 3: 385. 1893; Fl. Malay Penins. 4: 294. 1924. — *Musa truncata* Ridl., J. Fed. Malay States Mus. 4: 80. 1909; Fl. Malay Penins. 4: 294. 1924.

Description.

Perennial herb, pseudostems 1.4–7 m tall, 17–65 cm in circumference, light green, green yellow to medium green, sap ivory, young sucker 1–6, leaves with or without blotches. Petiole 16–130 cm long, base with small to large dark purple-brown blotches, petiole canal margins curved inward, straight or open with margins spreading. Leaf blades oblong, 80–340 by 25–95 cm, underside slightly waxy to very waxy, base cuneate, oblique, rounded, cordate or auriculate, apex prominently blunt. Inflorescence hanging vertically to curved or at an angle downward; basal flowers male, sterile; terminal flowers female, sterile, *peduncle* glabrous to slightly hairy to very hairy with short hairs, 8–72 cm. Female inflorescence fusiform to conical, 20–40 cm by 10–15 cm; apex acute; bracts lanceolate to elliptical; apex acuminate or acute, apex overlapped or not, revolute before falling; externally dark purple, purple, red-purple, purple-brown, red, orange-red or yellow sometimes with yellow streak; internally red-purple, red, pink-purple, purple, orange-red, ivory or yellow. Male inflorescence ellipsoid to conical to ovate, 10–24 cm by 4–10 cm; apex acuminate, acute to obtuse; bracts ovate; apex acuminate, acute or obtuse, apex overlapped or not, revolute before falling; externally dark purple, purple, red-purple, purple-brown, red, orange-red or yellow, sometimes with yellow apex and yellow streak; internally red-purple, red, pink-purple, purple, orange-red, ivory or yellow. *Female flowers* compound tepal ivory, sometimes with pink flush, lobes yellow; adaxial inner tepal ovate; ovary green; stigma ivory. *Male flowers* compound tepal ivory, lobes yellow; adaxial inner tepal elliptic; ovary ivory; stigma yellow to orange. *Bunch* horizontal, slightly angled downward or upward or descending vertically; male bracts persistent or not after anthesis, 9–53 cm, hands per bunch 3–15, fruits per hand 5–23. *Fruits* biseriate, pedicel length 0.3–2 cm, 5–12 cm by 1.5–2.5 cm, apex bottle-necked, 0.4–1.5 cm. Seeds irregular, angular, rough surface, brown to black.

Distribution.

India (Assam), Myanmar, China, Malaysia, Indonesia, Australia (Queensland), Polynesia.

Notes.

The widest distributed species in Thailand, with four recognised subspecies, one in the north and central plain to the eastern parts of the country and three mainly in the south. Approximated dispersal boundaries of each

subspecies can be drawn; therefore, the rank “subspecies” is preferred rather than “variety.” Meanwhile, hybrids discovered at each boundary indicated the close relationship between them.

Key to subspecies of *M. acuminata*

1. Leaf base cuneate to oblique, bract apex overlapping 1–2 cm, external bract red-purple to purple brown, rarely yellow..... *Musa acuminata* subsp. *siamea*

1. Leaf base round, cordate or auriculate, bract apex not overlapping or overlapping less than 1 cm, external bract dark purple, purple, red-purple, red to orange red, rarely yellow..... 2

    2. External bracts dark purple, internal bract ivory to pale red-purple fading to ivory at the base.....*Musa acuminata* subsp. *truncata*

    2. External and internal bracts purple, red-purple, red to orange red, rarely yellow 3

        3. Rachis horizontal to falling vertically, bud direction downward .... *Musa acuminata* subsp. *malaccensis*

        3. Rachis thick, horizontal to upward, bud direction horizontal to upward ..... ***Musa acuminata* subsp. *kraburiensis***

subsp. **kraburiensis** Swangpol & Somana, **subsp. nov.**, Figure 10.

Description.

Pseudostem 1.7–4.0 m tall, 25–50 cm circumference. Young plants sometimes with sparse purple blotched leaves. *Leaves* 105–250 cm by 40–95 cm, upper surface little or not waxy; base rounded, cordate or auriculate; petiole 60–100 cm long; petiole canal transverse section straight with erect margin. *Female inflorescence* peduncle 15–40 cm, sometimes with short hairs; fusiform to conical, 20–40 cm by 10–15 cm. *Male inflorescence* lanceolate to ellipsoid to ovate, 10–20 cm by 6–10 cm; bracts convolute, externally and internally often purple, red-purple, pink-purple to orange-red, rarely yellow, externally sometimes with yellow or red purple streaks and very little wax; bract revolute before falling. *Rachis* at anthesis horizontal or angled upwards, rachis circumference usually more than 3 cm, prominent bract scars. *Infructescence* 4–15 hands per bunch, 5–24 fruits per hand, biseriate. *Fruit* pedicel length 0.5–1.0 cm, 2–10 cm by 1.3–3.0 cm, curved to straight, fruit transverse section rounded to slightly ridge, apex bottle-necked, 0.5–1.5 cm. Seed angular, rough surface, dark brown.

Thailand.

PENINSULAR: Chumphon (Pathio, Tha Sae, Mueang Chumphon, Sawi, Thung Tako, Lang Suan, Lamae, Phato), Ranong (Kra Buri, La Un, Mueang Ranong, Kapoe, Suk Samran).

Distribution.

Endemic to the Kra Isthmus, ca. 9 – 10.5°N of the peninsular Thailand on the Tanao Si/Tenasserim mountain chain. The northern border of the distribution area is in Amphoe Pathio to Phato, Changwat Chumphon and ends in Amphoe Suk Samran, Changwat Ranong.

Ecology.

Scatter populations of this species are found on hills, slopes, and open areas near streams along Route No. 4, No. 4006 and in fruit orchards in Amphoe Lang Suan.

Vernacular.

Kluai Pa Kraburi (“wild banana from Kraburi” — in Thai).

Notes.

The Kra Isthmus area where this subsp. *kraburiensis* was found at the biogeographic transition zone of two floristic provinces, Indochinese and Sundaic (Woodruff 2003). The subspecies is possibly the natural fertile hybrid which connects the subsp. *siamea* at the southernmost end of its distribution boundary to the northernmost area of the subsp. *malaccensis* in the Thai peninsular. At the borderline in Amphoe Tha-Sae, Changwat Chumphon, there are also *siamea-kraburiensis* hybrid-like plants, meanwhile, in Amphoe Lang Suan and Amphoe Phato of Changwat Chumphon, subsp. *kraburiensis* grows alongside subsp. *malaccensis*. A yellow bract form of this subspecies is found in Changwat Ranong.

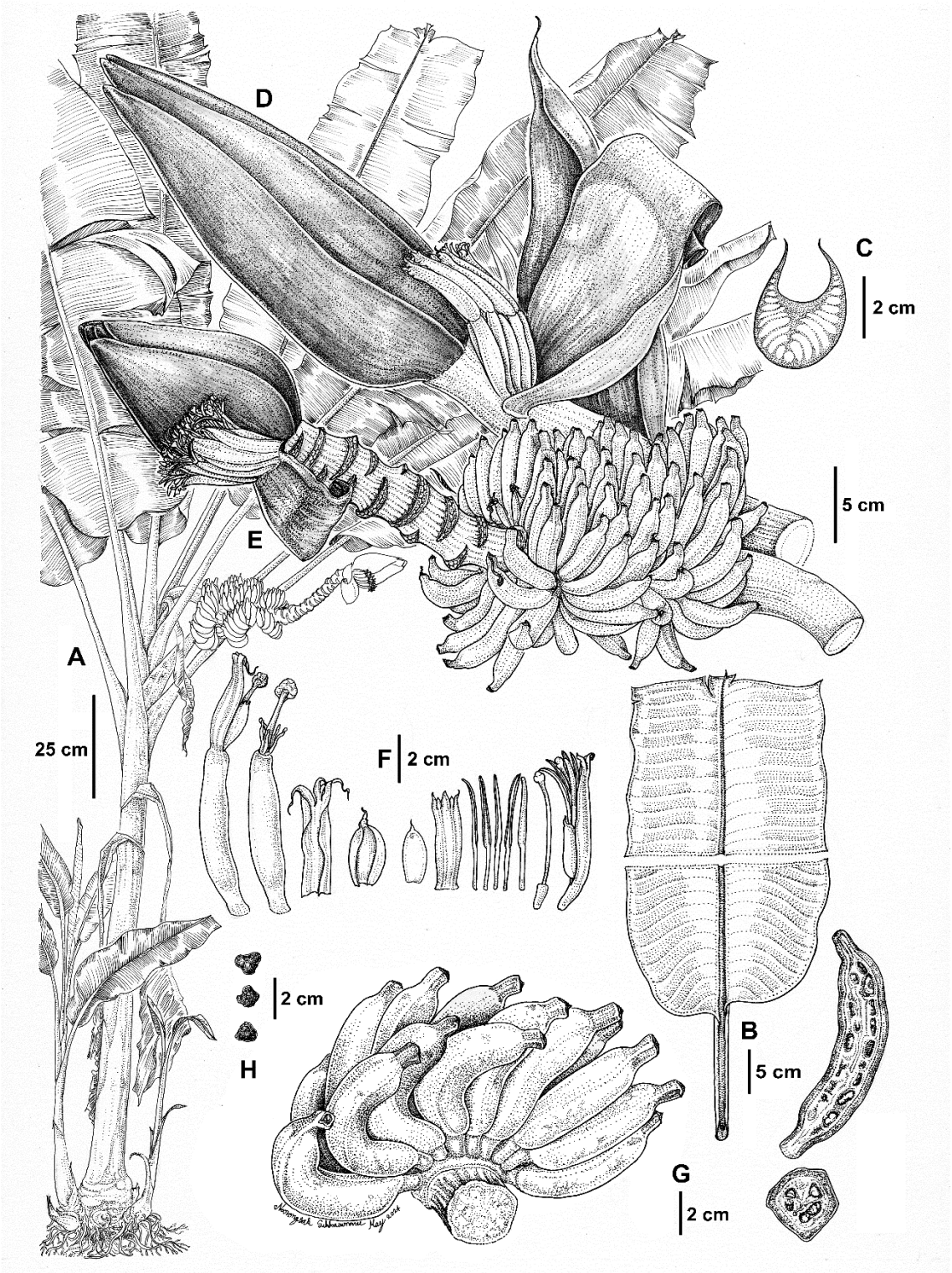

Figure 10. *Musa acuminata* subsp. *kraburiensis* Swangpol & Somana, subsp. nov. (A) clump; (B) a leaf showing base and apex; (C) a transverse section of the petiole; (D) a female inflorescence; (E) a male inflorescence; (F) flowers showing (from left to right) a female flower, a female flower without the tepals, a compound tepal and a free tepal of a female flower, a free and a compound tepals of a male flower, five anthers, a pistil, and a male flower; (G), left, a hand of fruits and, right, a transverse and longitudinal sections of fruits. Illustrated by N.S.; graphic by S.C.S. and W.I.

Key to forma of *M. acuminata* subspecies *kraburiensis*

1. Bract red, orange-red, red purple or pink-purple ..... **f. kraburiensis**
1. Bract yellow ..... **f. luteola**

a. **f. kraburiensis** Swangpol & Somana, **form. nov**. Holotype: SS & JS 689, BKF, Ranong, Kapoe, Muang Kluang, 15 Dec 2023; Isotype: SS & JS 599, BKF, Chumphon, Lang Suan, Wang Ta-ko, female inflorescence, 24 Sep 2016, SS & JS 599, BKF; male inflorescence, Ranong, Kapoa, Muang Kluang, BKF.

Description.

Male bract usually red or orange-red, but sometimes red-purple to pink-purple

b. **f. luteola** Swangpol & W.Inta, **form. nov**. Holotype: SS & JS 690, BKF, Ranong, Kapoe, Muang Kluang, 15 Dec 2023. Isotype: SS & JS 601, BKF, Ranong, Mueang, Ratchakrut, Ban Khlong Phai, 24 Sep 2016; SS & JS 251, BKF, Ranong, Mueang, Ratchakrut, Ban Khlong Phai, 17 Apr 2009.

Description.

Male bract yellow.

Thailand.

PENINSULAR: Ranong (Ban Khlong Phai).

Distribution.

Endemic to only one location in Changwat Ranong The authors estimated that no more than 30 clumps of this yellow bract forma sparingly grown on hillside in an area of approximately 10 km^2.

Vernacular.

Kluai Pa Kraburi Pli Lueang (“wild banana from Kraburi with yellow buds” –in Thai), Kluai Pa Kraburi Si Thong (“golden wild banana from Kraburi” –in Thai)

Notes.

The plant is possibly a natural mutant of *M. acuminata* subsp. *kraburiensis*. In our observations, the yellow bract forma attracts squirrels, birds and insects indifferently from the red bract counterpart, however, the former seems intolerant to strong sunlight, weaker and outnumbered by the latter. The population is highly threatened by land clearing for agricultural purposes and road expansions.

subsp. **malaccensis** (Ridl.) N.W.Simmonds, Kew Bull. 11, 3, 1956: 463–489. — *Musa malaccensis* Ridl., Trans. Linn. Soc. London, Bot. 3: 385. 1893. — *M. acuminata* Colla, the Selangor form, Cheesman, Kew Bull. 3, 1, 1948, Simmonds, Malayan Nat. J. 10, 3, 1955; *M. acuminata* Colla, the Kedah form, Simmonds, Malayan Nat. J. 10, 3, 1955. — *Musa acuminata* var. *malaccensis* (Ridl.) Nasution, Mem. Tokyo Univ. Agric. 32: 75. 1991. — *Musa flava* Ridl., Trans. Linn. Soc. London, Bot. 3: 385. 1893.

Description.

Pseudostem 1.7–3 m tall, 20–65 cm circumference. Leaves 105–340 cm by 40–95 cm, slightly waxy; base rounded, cordate or auriculate; petiole 40–130 cm long. Female inflorescence fusiform to conical, 20–40 cm by 10–15 cm. Male inflorescence ellipsoid to conical to ovate, 10–21 cm by 4–9 cm; bracts convolute to very slightly overlapped, externally and internally often red or orange-red, but sometimes red-purple to pinkish-purple or yellow, externally sometimes with yellow apex and yellow streak. Rachis horizontal, slightly angled downwards or upwards or descending vertically. Fruits biseriate, pedicel length 0.5–2 cm, 4–12 cm by 1.5–2.5 cm, apex bottle-necked, 0.4–1.5 cm.

Ecology.

Open areas at the edge of the forest, from 10–780 m asl.

Thailand.

NORTHERN: Tak (Doi Musoe, Along the Road Nos. 105 and 1090, Namtok Pa Wai), Mae Hong Son (Ban Mae Sam Lap); PENINSULAR: Surat Thani (Surat Thani Rubber Research Station, Along the Road No. 401), Phangnga (Lam Pakarang, Khao Lak-Lam Ru NP, Along the Road No. 4), Phuket (Along the Road No. 402), Krabi (Wat Tham Suea, Khao Phanom Bencha Forest Park, Tha Pom Klong Song Nam), Nakhon Si Thammarat (Along the Road No. 401, Namtok Phrom Lok), Phatthalung (Khao Pu - Khao Ya NP, Khao Chai Son), Trang (Namtok Sai Rung), Satun (Namtok Than Plio, Thale Ban NP), Songkhla (Along the Road No. 42, Namtok Ton Nga Chang, Khao Kho Hong), Pattani (Namtok Mai Khao), Yala (Namtok Sukthalai, Betong Hospital, Along the Road No. 401), Narathiwat (Hala-Bala Wildlife Sanctuary).

Distribution.

Malaysia [Selangor, Pahang (Type)], Indonesia (Sumatra, Mentawai, Krakatoa, West Java).

Vernacular.

Kluai Thuean and Kluai Pa, both mean “wild banana” –in Thai, Kluai Pa Malaka (“wild banana from Malacca” –in Thai)

Notes.

This species is widespread throughout Peninsular Thailand and has recently been documented in new locations within the northwestern provinces, but absent from the south-western and central areas. It is expected to be found across the border in Myanmar on the western side of the Tenasserim Range.

subsp. **siamea** N.W.Simmonds, Kew Bull. 11, 3: 463–489. 1956. — *M. acuminata*, the Annam form of Cheesman, Kew Bull. 1948, 27. — *M. acuminata*, the Annam form of Cheesman, Kew Bull. 1948, 27. — *M. acuminata* subsp. *burmannica* N. W. Simmonds, Kew Bull. 11, 3: 463–489. 1956.

Description.

Pseudostem 1.5–5 m tall, 20–60 cm circumference, light green, green yellow to medium green. Young sucker 1–6, with or without leaf blotch. Leaves 80–310 cm by 20–85 cm, hardly to very waxy; base oblique with left side cuneate, right side rounded; petiole 20–95 cm long, with or without large dark purple brown blotches, petiole canal with erect margins. Peduncle very hairy, short hairs, similar to velvet touch. Female inflorescence fusiform to conical, 20–40 cm by 10–15 cm. Male inflorescence conical to ellipsoid, 11–24 cm by 4–10 cm; apex acuminate to acute to obtuse, slightly to greatly overlapped; bracts ovate; apex acute to obtuse, revolute before falling, externally purple, purple-brown, red-purple to pink-purple or yellow, sometimes with a yellow apex, with very little or no visible sign of wax, internally red-purple, purple-brown to pinkish purple or yellow. Bunch horizontal descending vertically; male bracts persist or not after anthesis, hands per bunch 4–15, fruits per hand 5–26. Fruits biseriate, pedicel length 0.5–1.6 cm, 5–12 cm by 1.5–2 cm, apex bottle-necked.

Notes.

Type K! locality unspecified (I.C.T.A. Intro. 403, now maintained as the clone Siam).

Key to forma of *M. acuminata* subspecies *siamea*

1. Male inflorescences on one rachis numerous ..... **f. nanakornii**
1. Male inflorescence on one rachis one 2

2. Bracts purple, bluish purple to purple brown..... f. siamea

2. Bracts yellow ..... **f. byssina**

a. f. byssina Swangpol & Athawongsa, **form. nov.** Holotype: SS & JS 173, BKF, Nakhon Ratchasima, Pak Chong, Wang Katha, Ban Pa Kluai, 20 Jan 2006; Isotype: SS & JS 177, BKF, Chanthaburi, Pong Nam Ron, Thap Sai, Khlong Tani, 21 Jan 2006; SS & JS 224, BK, Nakhon Ratchasima, Wang Nam Khieo, Lam Phra Phloeng Dam, 13 May 2006. BK, SS & JS 307, KamPhaeng Phet, near Mae Wong NP, 31 May 2007.

Description.

Male bracts yellow.

Thailand.

NORTHERN: Kamphaeng Phet (near Mae Wong NP); EASTERN: Nakhon Ratchasima (Ban Pa Kluai, Lam Phra Phloeng Dam); SOUTHEASTERN: Chanthaburi (Khlong Tani).

Distribution.

Endemic to Thailand. Found scarcely in Central plain and Changwat Chanthaburi.

Ecology.

Grows in shades at the edge of the forest and in disturbed areas, on low slopes or open areas.

Etymology.

Byssina, the yellow colour of the raw silk cocoon, represents the plant's inflorescence bract colour.

Vernacular.

Kluai Pa Pli Leung ("yellow bud banana" — in Thai), Suwannakhattali ("golden banana" — in Thai), Kluai Pa Mai Thong ("golden silk banana" — in Thai)

Notes:

A yellow mutant occurring naturally, but rarely. The degree of yellowish-pink colour varies from those specimens found in Kamphaeng Phet, Nakhon Ratchasima and Chanthaburi and suspected as unrelated mutants.

b. f. nanakornii Swangpol, Chom. & Sukkaew., **form. nov.** –Musa acuminata subsp. siamea 'Kluai Roi Pli', Chomchalow et al., Acta Hort. 1026 (17–28), 2014. Holotype: N. Sukkaewmanee s.n., BKF, Phetchabun, Khao Kho, Khek Noi, Huai Nam Khao, 2 Feb 2006; Isotype: SS & JS 442, BKF, Tak, Phop Phra, Khiri Rat, 4 Oct 2010; SS & JS 502, BK, Nan, Na Noi, Santha, Ban Saen Suk, 23 July 2012, Fig. 11.

Description.

Male inflorescences per rachis numerous, each with long rachilla branches from each flower bud. Female flowers, mostly infertile, occasionally produce fruits with a few seeds.

Thailand. In cultivation.

Distribution.

Northern and Northeastern Thailand (Tak, Phetchabun and Nan). Probably also in Laos.

Etymology.

The forma name is dedicated to Dr. Weerachai Nanakorn, former President of the Botanical Society under HM Queen Sirikit of Thailand Patronage and former and established Director of the Queen Sirikit Botanic Garden (QSBG) who introduced this clone into cultivation at QSBG in 2009.

Vernacular.

Kluai Roi Pli (“one-hundred-bud banana” — in Thai), Kluai Khom Raya (“chandelier banana” — in Thai)

Notes.

The banana is a natural mutant. Its numerous male inflorescences differentiated from the original male flowers with extended rachillas, short and long. All accessions found in three provinces were grown by Hmong hill-tribe villagers as an ornamental plant. The male inflorescences are sometimes eaten as it is believed to promote fertility in both men and women.

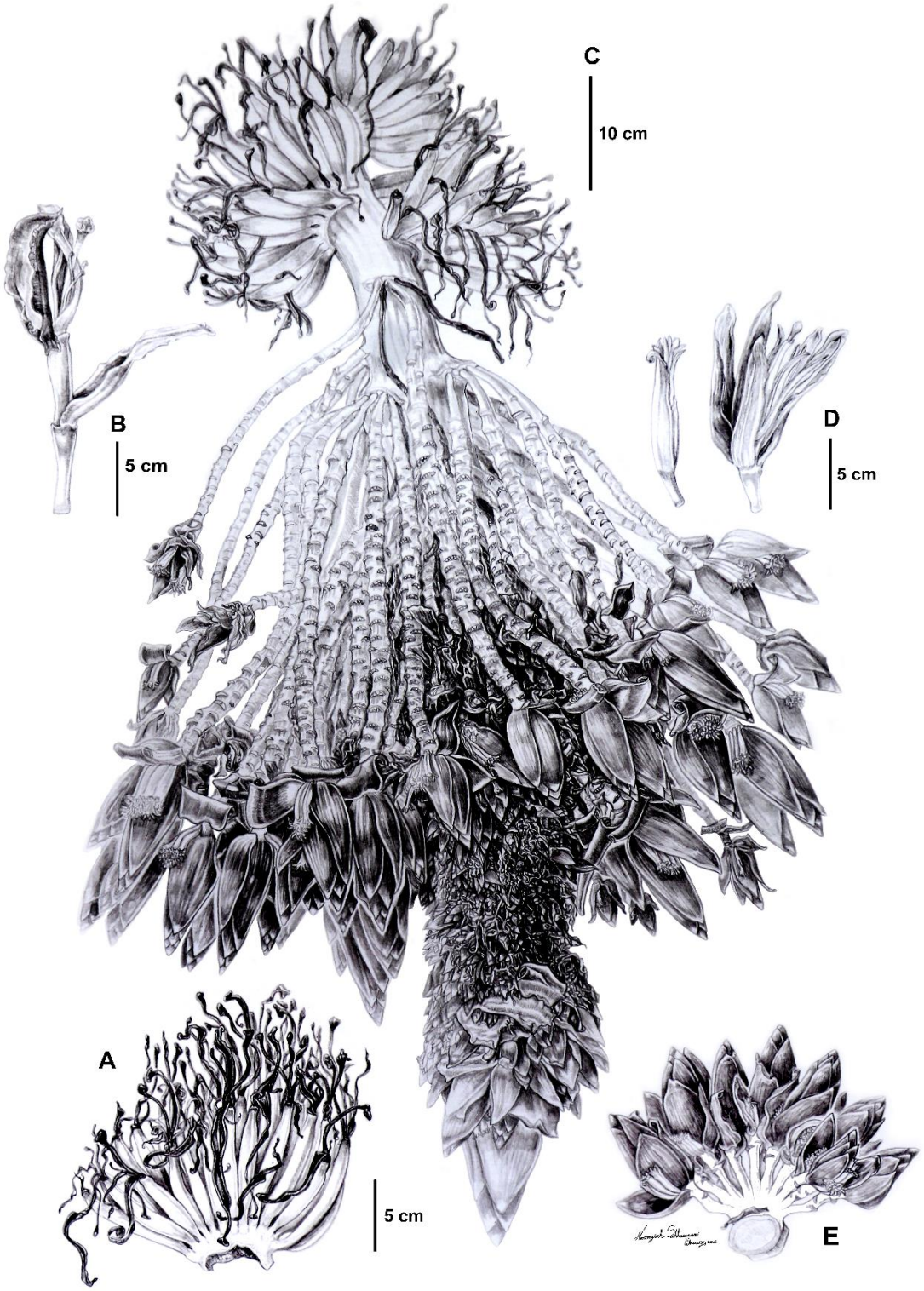

Figure 11. *Musa acuminata* subsp. *siamea* f. *nanakornii* Swangpol, Chom. & Sukkaew., form. nov. (A) a hand of withering female flowers; (B) an aberrant female flower; (C) an inflorescence with hands of aborted female flowers and a primary male inflorescence with numerous hands of secondary male inflorescences on extended

rachilla; (D) two male flowers, (left) a normal and (right) an abnormal one; and (E) a hand of secondary male inflorescences without extended rachilla. Illustrated by N.S.; graphic by S.C.S. and W.I.

c. f. siamea N.W.Simmonds

One male inflorescence per rachis. *Male bracts* purple, purple brown, red purple to pink purple.

Thailand.

NORTHERN: Chiang Mai (Doi Inthanon, Hot, Fang), Mae Hong Son (Mae La Noi), Tak (Umphang, Mae Ramat), Lampang (Chaehom); SOUTH-WESTERN: Kanchanaburi (Sangkhlaburi, Thong Pha Phum); CENTRAL: Saraburi (Kaeng Khoi).

Distribution.

Myanmar, Thailand, Laos, Cambodia, Vietnam, China.

Ecology.

Grows at the edge of the forest and in disturbed areas, on low slopes or open areas.

Vernacular.

According to Simmonds (1956), there are several vernacular names for wild banana in Thailand: Kluai Pa (general Thais) and Kluai Thuean (far southern Thailand), both signifying “wild banana;” Kluai Ling (“monkey banana” from Uttaradit); Kluai Mon (northern Thailand, Chiang Mai), where “Mon” could refer to the local tribal people at Thailand-Myanmar border. Kluai Khae, also translated to “wild banana” is used by northern Thais

Notes.

M. acuminata subsp. *burmannica*, though listed in previous literature as native to Thailand, was not found and believed to be a synonym of *M. acuminata* subsp. *siamea.*

subsp. truncata (Ridl.) Kiew, **loc. nov.** Ann. Bot. 88, 6: 1025. 2001. –*Musa truncata* Ridl., J. Fed. Malay States Mus. 4: 80. 1909; Cheesman, Kew Bull. 3(1): 17–28, 1948. — *Musa acuminata* subsp. *microcarpa* (Becc.) N.W.Simmonds, Kew Bull. 11(3): 463–489. 1956. — *Musa acuminata* Colla, the Camerons form, of Simmonds, Malayan Nat. J. 10, 3. 1955. — *Musa acuminata* var. *zebrina* (Van Houtte ex Planch.) Nasution, J. Biol. Indonesia 1: 282. 1993, Fig. 12.

Description.

Pseudostem 3–6 m tall, 30–45 cm circumference, light green. Young sucker 2–4, with or without large blotches. Leaves 155–245 cm by 55–75 cm, very little or no visible sign of wax; base oblique with both sides round, sometimes left-handed (the left-side base higher than the right-side one); petiole 50–100 cm long, with small to large dark purple-brown blotches, petiole canal straight with erect margins. Peduncle slightly hairy to very hairy with short hairs. Female inflorescence fusiform to conical, 20–40 cm by 10–15 cm. Male inflorescence elliptic, 10–20 cm by 6–10 cm, apex acute, convolute with very little or no visible sign of wax; bracts ovate, acute, revolute before falling, external dark purple, no yellow at the tip, internally ivory. Bunch horizontal or slightly angled downward descending vertically; male bracts not persistent after anthesis; hands per bunch 4–15; fruits per hand 15–28. Fruits biseriate, pedicel length 1.2–2 cm, slender, 10–12 cm by 1.5–2 cm, apex bottle-necked.

Thailand.

PENINSULAR: Narathiwat (Sukhirin, close to Hala-Bala Wildlife Sanctuary Wang, Ban Sai Borisat, Namtok Chat Warin Sungai Padi, along highway no. 4077 Sri Sakorn), Yala (Betong, KERR 7643, BM), Songkla (Ban Pian, KERR 14821 BM).

Distribution.

Malaysia [Selangor, Pahang (Type), Perak, Terengganu, Kedah; Borneo, Kinabalu and Sarawak].

Ecology.

Hill and montane tropical forests, 90–750 m alt.

Etymology.

truncata refers to “apex truncate” (square end of the leaves; Ridley, 1909).

Vernacular.

Kluai Thuean (meaning “wild banana”) was used in southernmost Thailand as mentioned by Simmonds (1956) for *M. acuminata* subsp. *microcarpa* and referred to Kerr specimens in which this vernacular name was applied to both *M. acuminata* subsp. *siamea* and *M. acuminata* subsp. *microcarpa*; Kluai Pa (also means “wild banana”), Kluai Pa Pli Muang (“purple-bud wild banana” – in Thai).

Notes.

A new record for Thailand. Simmonds (1956) has previously mentioned this Thailand native subspecies as *M. acuminata* subsp. *microcarpa*. Hybrids of *M. acuminata* subsp. *truncata* and *M. acuminata* subsp. *malaccensis* were found growing along in Changwat Yala. The hybrids possess bracts with intense red colour internally.

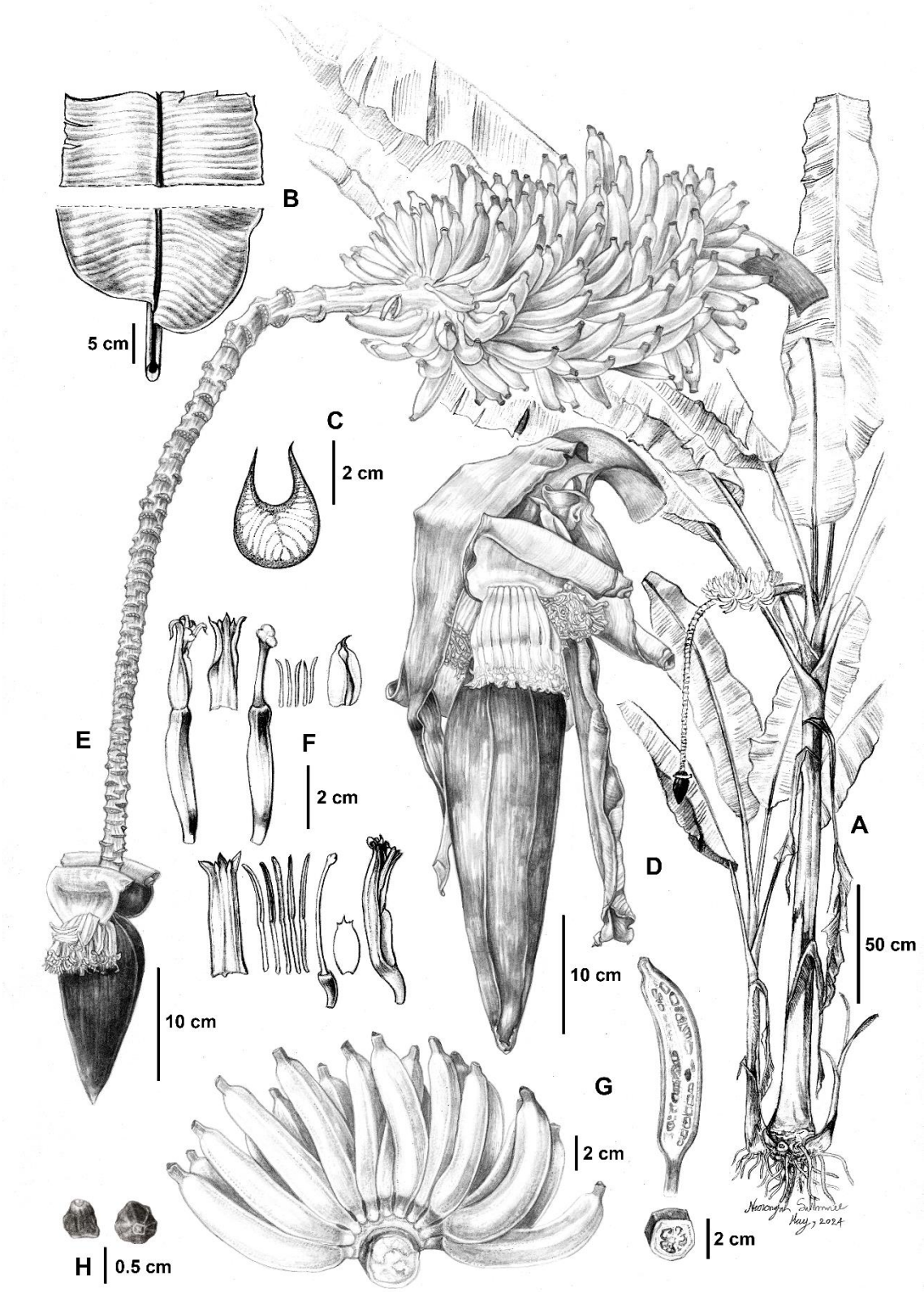

Figure 12. *Musa acuminata* subsp. *truncata* (Ridl.) Kiew, loc. nov. (A) clump; (B) a leaf showing base and apex; (C) a transverse section of the petiole; (D) a female inflorescence; (E) a male inflorescence; (F) flowers showing (upper from left to right) a female flower, and a compound tepal, a pistil, the five anthers, and a free tepal of a female flower, then (lower from left to right), a compound tepal, five anthers, a pistil, and a free tepal of a male flower and a male flower; (G), left, a hand of fruits and, right, a transverse and longitudinal sections of fruits. Drawn by N.S.; graphic by S.C.S. and W.I.

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Conflict of interest
The authors have declared that no competing interests exist.

Ethical statement
No ethical statement was reported.

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Author contributions
SCS and WI wrote the manuscript. All authors performed the taxonomic works and analyses, reviewed and approved the final version of the manuscript.

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