

## The history and identity of *Boesenbergia longiflora* (Zingiberaceae) and descriptions of five related new taxa

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**ABSTRACT.** The history of *Boesenbergia longiflora* (Wall.) Kuntze (Zingiberaceae) is reviewed, its identity is discussed and a lectotype designated. Five new, related taxa are described and illustrated: *B. collinsii* Mood & L.M.Prince, *B. hamiltonii* Mood, S.Dey & L.M.Prince, *B. kerrii* Mood, L.M.Prince & Triboun, *B. kingii* Mood & L.M.Prince, and *B. maxwellii* Mood, L.M.Prince & Triboun. A phylogenetic analysis of plastid *trnK* intron (including *matK*) and nuclear ITS DNA sequence data indicate these *Boesenbergia* species form a clade within *Boesenbergia*. Results of the molecular data analyses in concert with several diagnostic characters, support the recognition of the new taxa. Historical illustrations, colour plates, a field key to the species, a comparative table, a listing of the botanical history of *B. longiflora*, and a geographical distributional map are provided.

**Keywords.** Burma, *Curcumorpha*, *Gastrochilus*, India, Thailand

### Introduction

*Boesenbergia longiflora* (Wall.) Kuntze was described in 1829 as *Gastrochilus longiflora* by Nathaniel Wallich based on his collection from Rangoon, Burma [Wallich 6589A (K-W)]. *Boesenbergia* was proposed in 1891 when Otto Kuntze observed that *Gastrochilus* Wall. is a homonym of *Gastrochilus* D.Don (1825; Orchidaceae). In 1974 it was regarded as belonging to the monotypic genus *Curcumorpha* A.S.Rao & D.M.Verma. This change was countered by Larsen (1997) but is still in use by some (Kress et al. 2002, Gao et al. 2004).

During a botanical survey in the Lampang Province, Thailand in 1998, numerous plants which at first were identified as *B. longiflora* were observed growing on the margins of secondary forest. These were easily recognised by their robust stature and large, white flowers. Later, another *Boesenbergia*, reminiscent of *B. longiflora*, but with yellow flowers, was encountered on a limestone outcrop [Mood & Pedersen 1455 (C)].

Its specific identity remained unclear. Several years later, yet another *Boesenbergia* with yellow flowers was collected by Mark Collins (1963–2011) from a limestone area in Loei Province, Thailand. Living plants of this field collection (T-3068) were later determined to be similar to the earlier Lampang collection. Identification of the two collections began with a review of Wallich's description of *G. longiflora* which was described as having small, yellow flowers with red markings on the labellum (Fig. 1). This information was very surprising, as it was inconsistent with the current perception of *B. longiflora* being a ginger with large, white flowers with pink markings on the labellum (Wu & Larsen 2000; Kress et al. 2002; Gao et al. 2004, 2005; Larsen & Larsen 2006). This significant discrepancy precipitated a complete review of the history of *B. longiflora* (Appendix A).

The historical findings indicated that the true *B. longiflora* (Wall.) Kuntze was very similar to the two aforementioned Thailand collections. The current perception of a white-flowered ginger appears to have been fostered by a watercolour published by Hooker in 1843 (Fig. 2). Based on a reference by Baker (1890), the plant Hooker used for this illustration was sent to Kew from the Calcutta Botanical Gardens (Wallich 1840), which was identified with the unpublished name, *G. jenkinsii*. Although Baker (1890) mentioned this error, he described white flowers, as did Schumann (1904). Holttum (1950) also noted the discrepancy between the Hooker illustration and Wallich's, but did not pursue the matter. Rao and Verma (1974) described their *C. longiflora* as white-flowered, but in this case, it was based on 20 specimens from Assam and Meghalaya, India, the area where Wallich found *G. jenkinsii* (Voigt 1845).

Although the historical information improved the taxonomic understanding of *B. longiflora*, several taxa remained unconfirmed or unidentified: Wallich's *G. jenkinsii* from Assam (Fig. 2); the large white-flowered *Boesenbergia* common to N. Thailand; the specimens cited by Rao and Verma; and finally, the two yellow-flowered Thailand collections. In order to properly identify these and other specimens, the present research was initiated in 2008 using an integrated taxonomic/phylogenetic approach.

## Materials and methods

**Taxonomy.** Historical references, both text and illustrations (Appendix A) were used to provide an understanding of past taxonomic perceptions. Also, over 200 digital images of *B. aff. longiflora* obtained from various sources were reviewed and categorised by flower morphology and geographic location, providing early clues on diversity and phytogeography. Herbarium specimens (75) labelled as *B. longiflora* or *C. longiflora* were examined and photographed at ASSAM, BK, BKF and CAL in 2009. Another 75 specimens were viewed via digital images from AAU, C, E, K, L, P, SING and US. This exercise provided an important finding—the *B. longiflora* complex was extremely difficult to sort out and distinguish one taxon from the other in the herbarium. Vegetative characters often used to determine the identity of dried specimens in other Zingiberaceae were not particularly useful here. Additionally, flowers did not preserve well, changed colour upon pressing and became indistinguishable by shape.



**Fig. 1.** *Gastrochilus longiflora* (*B. longiflora*). Watercolour on paper by Vishnupersaud (1829) from the Wallich Collection, Kew. Reproduced with permission of The Board of Trustees of the Royal Botanic Gardens, Kew.

To determine which taxon a *B. aff. longiflora* specimen belonged, the location, habitat, plant height, flower colour and underground morphology were important. Here, the “Additional specimens examined” under each described species are determined based on a combination of these parameters. The name *B. longiflora* (see “Taxonomy” below) is lectotypified.

During 2008–2012, c. 25 live rhizome divisions of *B. aff. longiflora* were obtained from a variety of sources: botanical gardens, research institutions and various personal collections. Each accession was grown by the first author in Hawaii, USA under controlled, shade-house conditions. Details on the morphology and phenology were recorded over several growing seasons. DNA samples with a corresponding herbarium specimen were taken from each accession.

In 2009–2012 field observations were made in Thailand with botanists from BK, the Thailand Institute of Scientific and Technological Research and Kasesart University. Similarly in India, observations were conducted with personnel from the Botanical Survey India (Shillong), the Assam Forestry Department and the Nagaland University. Digital images of all *Boesenbergia* observed in the field and in cultivation were recorded for later reference.

Early in the research, all *Boesenbergia* species known to have radical inflorescences were evaluated for possible inclusion in the *B. longiflora* complex. Based on molecular data (Mood et al., unpublished) *B. basispicata* K.Larsen ex Siriruga, *B. tenuispicata* K.Larsen and *B. trangensis* K.Larsen belong to other *Boesenbergia* clades. DNA samples were not available for *B. angustifolia* (Hallier f.) Schltr., *B. phyllostachya* (Gagnep.) K.Larsen and *B. siphonantha* (King ex Baker) M.Sabu, Prasanthk. & Škorničk. Consequently, their phylogenetic position is undetermined at this time.

The final taxonomy presented here represents an incorporation of data from the phylogenetic analyses, field observations and detailed study of the cultivated plants. The descriptions are ordered with the yellow-flowered species first, followed by the white-flowered species. The distribution map (Fig. 20) was constructed by mapping types and selected specimens of each species (these are marked by an asterisk following the herbarium abbreviations in the list of additional specimens examined).

*Molecular phylogeny.* Phylogenetic analyses were conducted to complement and assist in taxonomic decisions required to elucidate relationships among species of the *B. longiflora* clade as defined here. Taxon selection was based on an unpublished broader analysis of plastid *trnK* data for *Boesenbergia* relative to other genera of Zingiberaceae (authors in prep.). The bulk of the data for non-*Boesenbergia* samples are from the earlier family-wide analyses of Kress et al. (2002) with a few additional sequences from recently described genera such as from Kress et al. (2010) and Leong-Škorníčková et al. (2011). The data for the specimens cited in these references can be found at <http://www.ncbi.nlm.nih.gov/genbank/> (GenBank 2011). A representative shortest maximum parsimony (MP) phylogram is shown in Fig. 3. Only names of relevant *Boesenbergia* samples are indicated on the phylogram.





**Fig. 2.** Hand-coloured lithograph published in Curtis's Botanical Magazine 69, t. 4010, 1843 as *Gastrochilus longiflora*. Reproduced with permission of The Board of Trustees of the Royal Botanic Gardens, Kew. (Identified by Baker (1890) as *G. jenkinsii*. Described here as *B. hamiltonii*.)

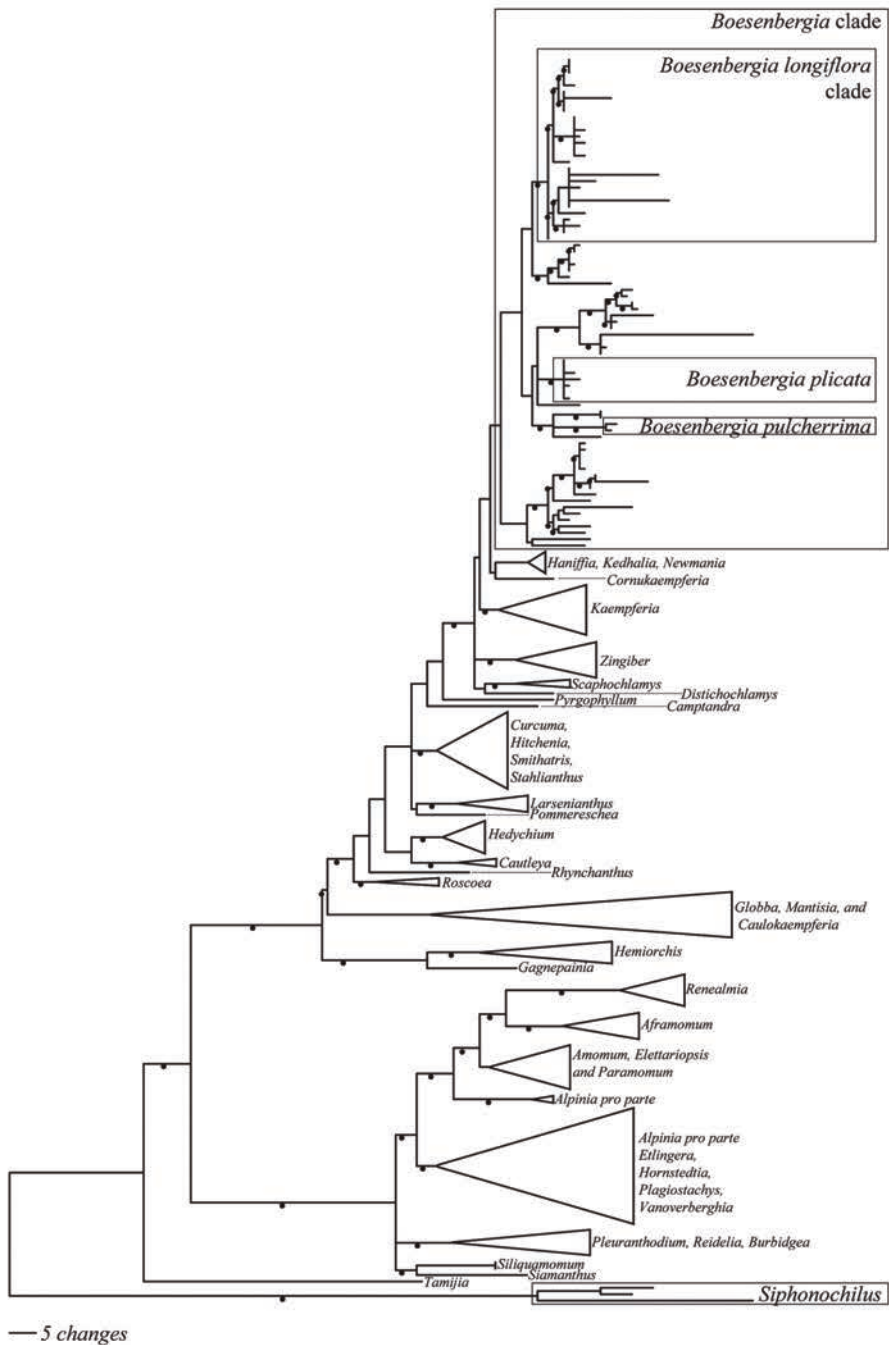
DNA was extracted from silica-dried leaf material or leaf tissue from herbarium specimens using standard methods as described in Kress et al. (2002). Thirty-seven samples of *Boesenbergia* were used in the DNA sequencing analyses. Two samples of *B. pulcherrima* (Wall.) Kuntze, the generic type, were designated as outgroup taxa. Two other samples, *B. plicata* var. *lurida* (Ridl.) Holttum and *B. plicata* var. *plicata* (Ridl.) Holttum were also included. The remaining samples were all members of the *B. longiflora* clade. All samples were designated by a collection or accession number and vouchered (Appendix B).

Both nuclear and plastid data were collected. The nuclear ribosomal ITS (nrITS) region was amplified using the 18S-F and 26S-R primers (Prince 2010) and Phusion high fidelity polymerase (New England BioLabs, Ipswich, Massachusetts, USA) with 5X GC Buffer per the manufacturer's instructions at an annealing temperature of 62°C. The same primers were used for subsequent sequencing. The plastid *trnK* region was amplified and sequenced using conditions described in Kress et al. (2002) or Prince & Kress (2006). Two newly designed primers were synthesized to assist with sequencing of some difficult samples (5Fb: CTCTATGGATTTTCAAGGAT and 5Rb: AGACCAAATGAAAATAATA). All samples were direct sequenced on a 3130xl Genetic Analyser at Rancho Santa Ana Botanic Garden (Claremont, California, USA).

Noisy sequences (electrophoregrams showing more than a few polymorphic sites) in the nrITS data were cloned using TOPO TA cloning kits (Invitrogen, now Life Technologies, Grand Island, New York, USA) with four to eight clones sequenced per sample. A small number of the *trnK* sequences were also noisy (due to polymerase "stutter" caused by a mononucleotide T repeat around 450bp). Those samples were re-amplified using Phusion polymerase, which has been shown to outperform other polymerases for this particular problem (Fazekas et al. 2010) and re-sequenced.

Individual sequences of each specimen were edited and a consensus sequence was generated in Sequencher v4.9 (Gene Codes Corporation, Ann Arbor, Michigan, USA). The consensus sequence was trimmed (18S and 26S data pruned from the ITS1+5.8S+ITS2 region, removal of amplification primer sequences from the *trnK* region) exported and aligned manually in Se-Al v2.0a11 (1996; available from A. Rambaut, Oxford, England, UK at <http://tree.bio.ed.ac.uk/software/seal>). Alignment was relatively straightforward due to the high degree of sequence similarity and length for the taxa involved. Ambiguous regions were generally restricted to the monomeric "T" repeat in the 5' *trnK*–*matK* intergenic spacer (IGS). All newly generated data have been deposited in GenBank and are available under accession numbers JX992748–JX992840 (Appendix B).

Data were analyzed under parsimony and likelihood criteria by genomic data partition, first independently, and later in combination. The decision to combine data partitions is often based upon the results of an incongruence-length difference, or ILD test (Farris et al. 1995). We did not perform this test as it has been suggested to be too conservative (Cunningham 1997, Struck 2007). We expected the test to fail due to the presence of two very different ITS copies detected for at least one sample in the ITS data partition. The decision to combine data partitions was instead based on a combination of tree topology congruence and branch support values. In most instances



**Fig. 3.** One of many shortest maximum parsimony phylograms (simplified) for *Boesenbergia* and other representatives of Zingiberaceae based on plastid *trnK* data analysis, rooted using *Siphonochilus* J.M.Woods & Franks as suggested by Kress et al. (2002). The position of the genus *Boesenbergia*, the *B. longiflora* clade and the taxa sampled for this study are indicated. • indicate branches with MP Bootstrap values  $\geq 50\%$ .



tree topologies were consistent between data partitions. In cases where tree topology differed, branch support for the conflicting topology was reviewed. If branch support was weak ( $<65\%$  BS,  $<0.95$  PP) the data for those taxa were analysed in combination. As stated above, the ITS data for one taxon included two very different copies. In another instance, there was strong positional conflict among the nuclear and plastid phylogenies for one sample. Disparate copies were included in all individual data set analyses, but only one copy was included in combined data analyses. The ITS copy retained for combined analyses was selected to best match to the chloroplast phylogeny.

Maximum parsimony and maximum likelihood (ML) analyses were conducted in PAUP\* (version 4.0b10, Swofford 2002). Heuristic search methods were conducted in each case with 1000 random addition replicates for MP and 10 random addition replicates for ML, each with tree bisection and regrafting (TBR) branch swapping. Maximum Parsimony analyses were conducted under Fitch parsimony criteria (Fitch 1971). Maximum likelihood analyses were conducted using model parameters selected by jModelTest (version 0.1.1 available at <http://darwin.uvigo.es>; Posada 2008, Guindon & Gascuel 2003) under both the Akaike Information Criterion (AIC; Akaike 1974) and the Bayesian Information Criterion (BIC; Schwarz 1978). All Maximum Likelihood trees were saved. Both AIC criterion and BIC criterion models were analysed for all data partitions, but only the trees from the AIC analyses will be discussed as both methods produced nearly identical trees.

Branch support was estimated using parsimony bootstrap (BS) in PAUP\* and posterior probabilities (PP) in MrBayes v3.2.1 (Ronquist & Huelsenbeck 2003). MrBayes analyses were conducted through the CIPRES portal (Cyberinfrastructure for Phylogenetic Research; Miller et al. 2010) and used partitioned data whenever appropriate (partitions = *5'trnK* IGS + *3'trnK* IGS, *matK*, ITS) and were run in triplicate to ensure convergence. Bootstrap values were based on 1,000 pseudoreplicates, each with 100 random addition replicates, TBR branch swapping, saving a maximum of 10 trees per random addition replicate and hold=4 trees. The number of generations necessary to estimate posterior probabilities varied depending upon the dataset and the time required to reach stasis (average standard deviation of the splits frequency  $<0.01$ ).

## Results and discussion

A number of exploratory analyses were conducted to evaluate the consistency of the phylogenetic hypotheses generated by the different data partitions. As stated above, some of the data generated from the nuclear ribosomal partition were noisy, indicating the presence of divergent ITS copies within a sample. Although it is not common, multiple copies of ITS have been detected in a number of genera and species of Zingiberaceae including *Alpinia* (Liu et al. 2009), and *Cornukaempferia* (L. Prince pers. obs.), and multiple ITS copies per individual is prevalent in *Curcuma* (Záveská et al. 2012) and *Kaempferia* (L. Prince, pers. obs.). The presence of multiple, strikingly different copies can be explained by a number of different evolutionary histories, a



few of which are presented here. The ITS region is present in hundreds (or thousands) of copies, often on multiple, different chromosomes. Processes affecting the utility of ITS for phylogenetic reconstruction were reviewed by Álvarez & Wendel (2003) including a discussion of the processes described below.

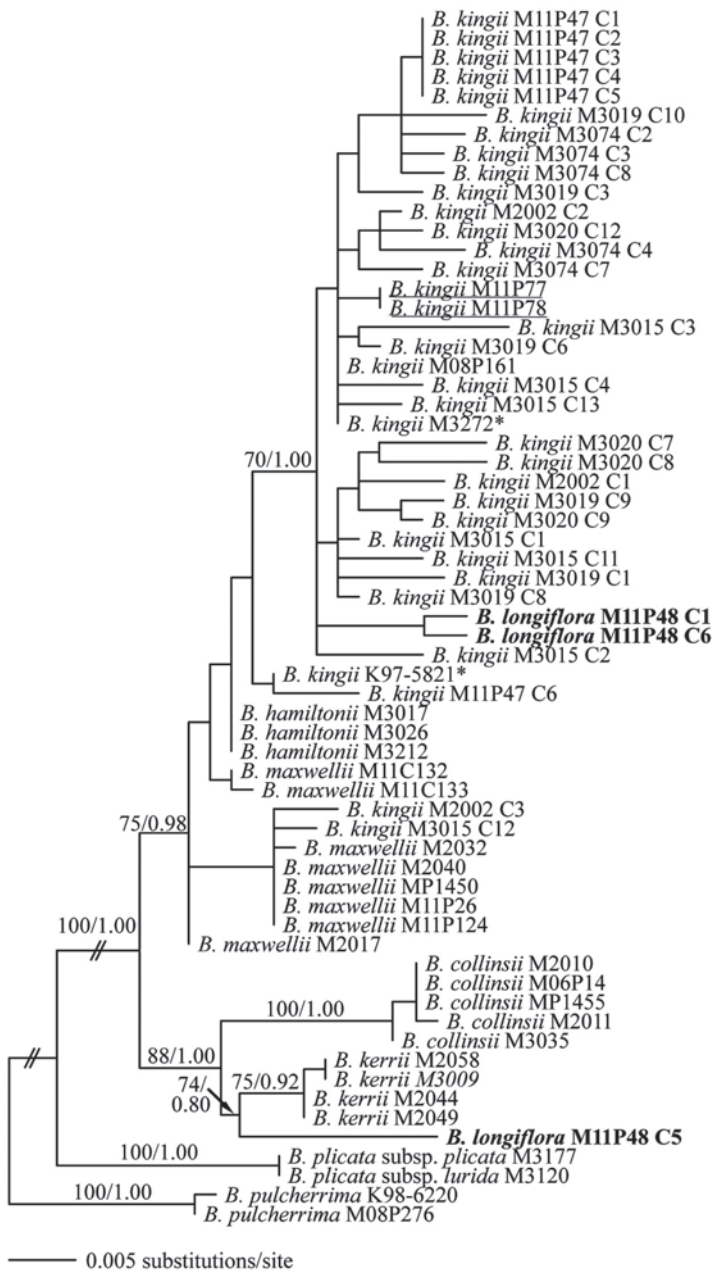
One explanation for the detection of multiple different copies in one organism is that the multiple copies were present in the ancestor and those copies are being maintained through time. Another explanation is recent genetic drift of some copies due to relaxed evolutionary constraints. Given the importance of this region for the functionality of the organism, it would not be likely unless there has been duplication (perhaps due to polyploidisation). Chromosome counts have not been made for the sample of *B. longiflora* (Kress 03-7305, US) included here, so perhaps this is a plausible explanation. Yet another possibility is recent gene flow between closely related taxa. If hybridisation happened in the recent past, there is a possibility that the two different copies have not yet had the time to undergo concerted evolution. If this process is incomplete, each parental copy will be recovered and, in a phylogenetic analysis, the different copies would each cluster with one of the (putative) parents. Alternatively, chimeric ITS sequences might be detected.

No matter the source of multiple, different copies of ITS present within any given organism, there is ample indication that most organisms undergo concerted evolution of the ITS region, a process by which the different copies are homogenised across the genome resulting in a single (or at least dominant) copy per organism. The length of time for complete homogenisation of the ITS of any given organism is unknown and likely highly variable. Although there has been a great deal of speculation regarding concerted evolution and homogenisation in purported hybrid taxa of flowering plants, our best understanding of the actual time required is gleaned from experiments with artificial hybrids (e.g., *Armeria*: Fuertes Aguilar et al. 1999, Feliner et al. 2001; *Hieracium*: Mráz et al. 2011) and in recently derived polyploidy taxa (e.g., *Spartina*: Ainouche et al. 2004; *Helictotrichon*: Winterfeld et al. 2009; *Oryza*: Ying et al. 2010).

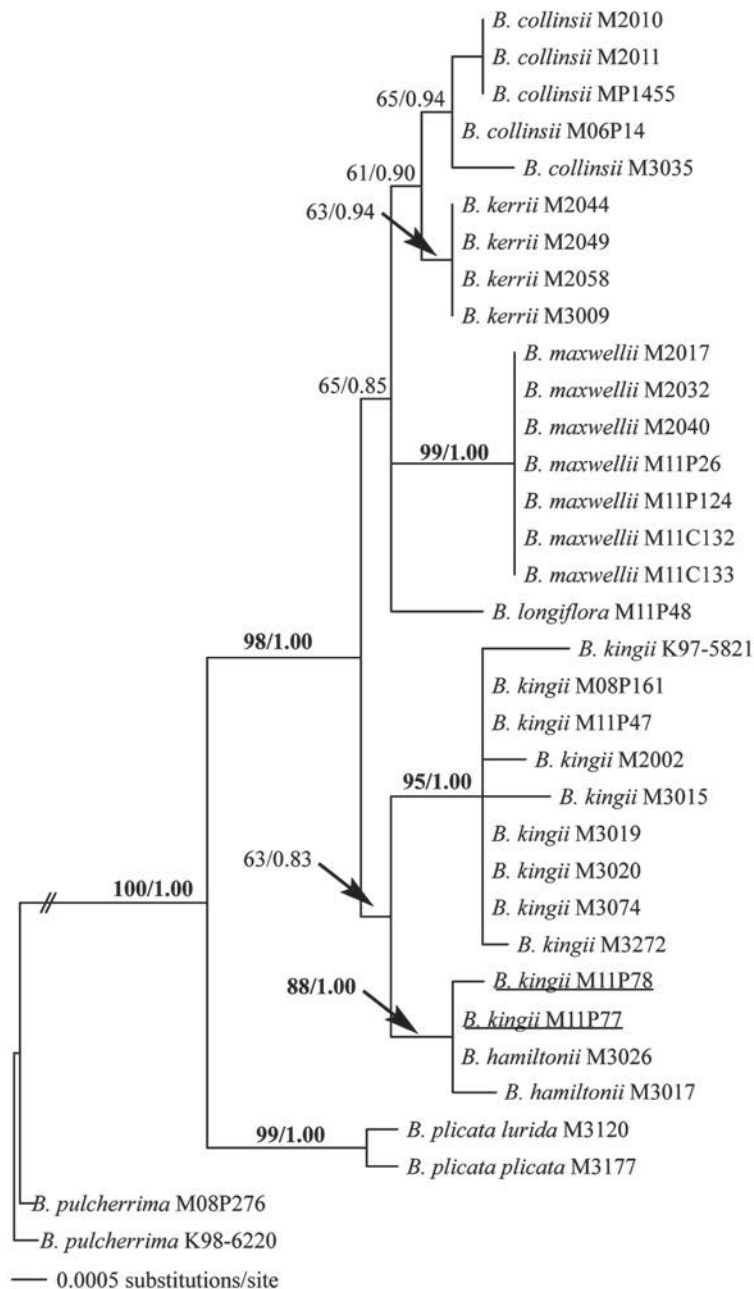
### ***Nuclear ribosomal ITS data***

The aligned data matrix included 86 potentially parsimony-informative characters (43 for ingroup only). As indicated above, several samples required cloning to obtain clean ITS sequences. Two other samples, indicated by an asterisk in Fig. 4, should be cloned to clarify a few polymorphisms. Maximum parsimony analysis produced over 100,000 shortest trees and could not be run to completion. One of the 37 shortest ML trees is shown in Fig. 4.

The ML phylogram presented in Fig. 4 identifies a moderately supported clade that includes all samples of *B. kerrii* and *B. collinsii* plus one of the *B. longiflora* clones (88% BS; 1.00 PP). Both *B. kerrii* and *B. collinsii* are resolved as monophyletic with moderate to strong support. The other ingroup clade is moderately to strongly supported (75% BS; 0.98 PP), and includes all samples of *B. kingii*, *B. hamiltonii*, *B. maxwellii* and two clones of *B. longiflora*. Resolution within the clade is poor and internal branches are generally poorly supported although most of the *B. kingii* samples and clones cluster together with 70% BS and 1.00 PP.



**Fig. 4.** One of 37 best, Maximum Likelihood phylograms ( $-\ln=2218.749$ ) for *Boesenbergia longiflora* and closely related taxa based on analysis of nuclear ribosomal ITS data for all samples and clones. Support values (Bootstrap/Posterior Probability) for critical branches are shown above branches. Bold typeface highlights strongly supported positions of the different *Boesenbergia longiflora* copies generated by cloning. Asterisks indicate samples that should also be cloned to clarify a few polymorphisms. Underlined samples are placed in conflicting positions on the chloroplast phylogeny. Note: lower branches were pruned to fit page and are not to scale.



**Fig. 5.** Single best Maximum Likelihood phylogram ( $-\ln=3953.067$ ) for *B. longiflora* and closely related taxa based on analysis of chloroplast *trnK* intron data. Support values (Bootstrap/Posterior Probability) for critical branches are shown above branches. Numbers in bold typeface indicate strong support. Underlined samples are placed in conflicting positions on the nuclear ribosomal phylogeny. Note: lower branches were pruned to fit page and are not to scale.

The identification of at least two disparate ITS copies for *B. longiflora* requires further discussion. Only one sample of *B. longiflora* was available for inclusion in this study. This sample, *M11P48* was from cultivated plants grown by the first author, but originally collected in Burma (*Kress 03-7305*, US). Multiple clones representing one *B. longiflora* ITS type were distributed among members of the *B. kingii* clade (ITS copy “A”) while the other *B. longiflora* copy fell sister to the *B. kerrii* clade (ITS copy “B”) as is shown in Fig. 4. Although a number of tests have been proposed to distinguish between the processes of hybridisation and incomplete lineage sorting (Joly et al. 2009) all have limitations. We were restricted here by the single sample for *B. longiflora*, but hopefully, more samples will be available for future analyses.

The majority of the polymorphic samples were identified as *B. kingii* based on morphology. Six of the twelve samples required cloning to generate clean ITS sequences. These samples fall into two categories. The first group included samples with multiple ITS sequence types, but those sequences were all quite similar with only a few different bases or slight length variations. Analyses of the ITS data partition placed all of these sequences in the *B. kingii* sensu lato clade as described above (*B. hamiltonii* + *B. kingii* + *B. maxwellii*), and with moderate to high support (75% BS, 0.98 PP) but with poor resolution within the clade (Fig. 4). Further, most of the *B. kingii* samples clustered with moderate support (70% BS, 1.00 PP). Among the ingroup members, *B. kingii* is the most broadly distributed species and is the most genetically diverse taxon.

#### ***Chloroplast trnK intron (including the protein coding matK gene)***

A total of 36 potentially parsimony-informative characters (15 for ingroup only) were used to generate almost 100,000 maximum parsimony trees. However, maximum likelihood analyses resulted in a single best tree (Fig. 5). The likelihood tree had a topology identical to several of the MP trees. As with the results of the ITS analyses, both MP and ML analyses identified two clades within the ingroup, one including samples of *B. collinsii* + *B. kerrii* + *B. longiflora* + *B. maxwellii* (65% BS; 0.85 PP) and a clade comprising *B. hamiltonii* and *B. kingii* (63% BS; 0.83 PP). Three taxa were resolved and supported as monophyletic: *B. collinsii* (65% BS, 0.94 PP) *B. kerrii* (63% BS, 0.94 PP) and *B. maxwellii* (99% BS, 1.00 PP). The relationship of *B. maxwellii* to *B. hamiltonii* and *B. kingii* differed here relative to the ITS results, but only with weak (65% BS; 0.85 PP) support. Sequences for two samples were not available for this data set, *B. hamiltonii* *M3212* and *B. maxwellii* *MP1450*. The two samples with names underlined in Fig. 4, *B. kingii* *M11P77* and *M11P78*, were identical and clearly supported as members of the *B. kingii* group in the phylogeny produced by analyses of the nuclear ITS dataset. Results of the chloroplast data analyses (Fig. 5) clearly (88% BS, 1.00 PP) placed these two samples in a clade with *B. hamiltonii*.

#### ***Combined analyses***

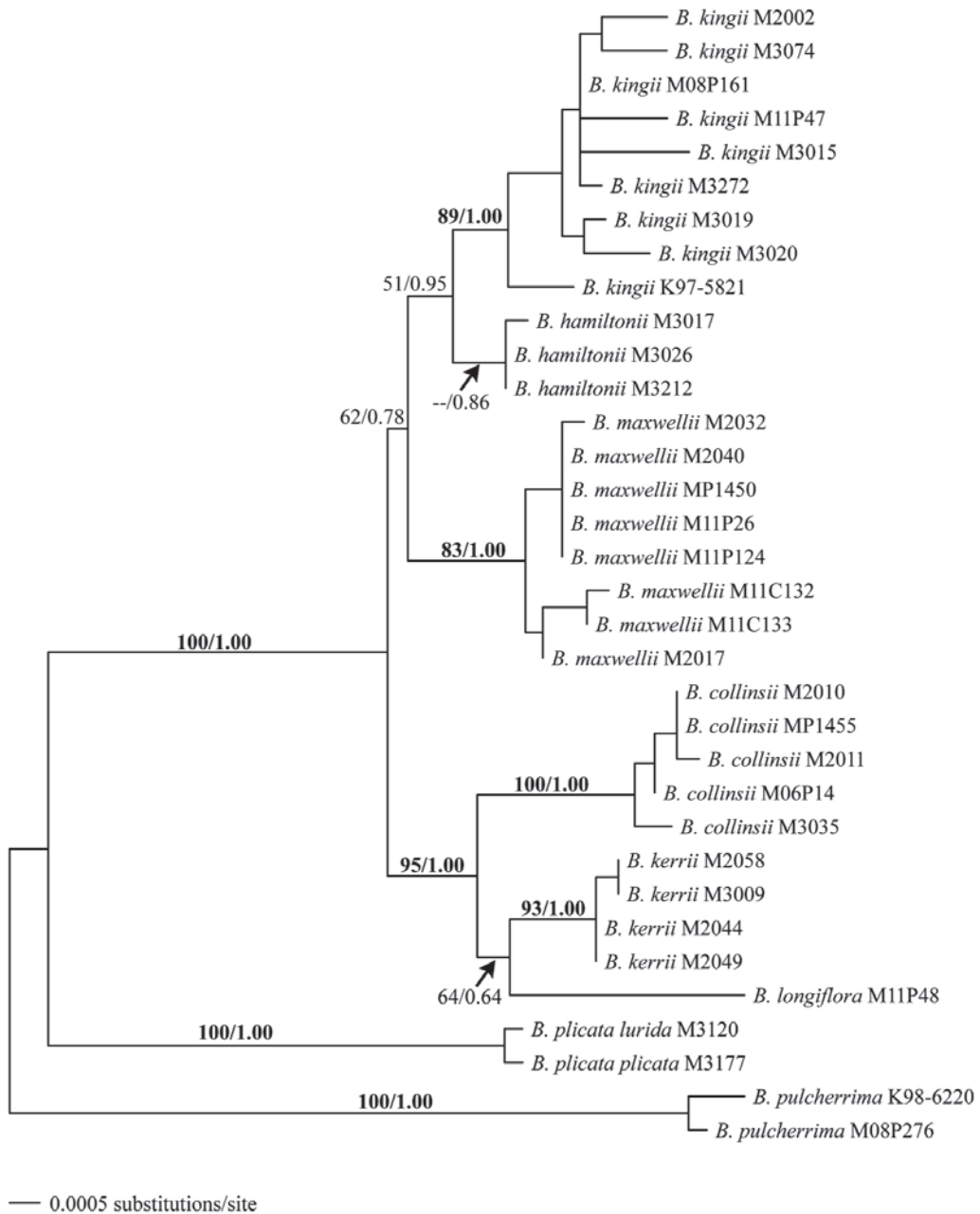
The combined data set required a number of samples to be excluded. Because the ITS data required cloning for some samples, results of the ITS MP analyses were used to select the clone with the shortest branch for each sample (as suggested by Beilstein et



al. 2008) for subsequent use in the combined analyses. This was done only when all clones for a particular sample either formed a monophyletic lineage or clustered within a moderately or well-supported lineage ( $BS \geq 75\%$ ). In the instance of *B. kingii* samples *M11P77* and *M11P78*, there was positional conflict between the nuclear and plastid datasets. Those samples were excluded from the combined analysis. As mentioned, there was only a single sample of *B. longiflora* available for this study. The nuclear data set included two distinctly different copies, A and B. Rather than totally exclude this critical taxon, we selected the nuclear copy B that best matched the chloroplast phylogeny, while recognising we do not know which better represents the evolutionary history of the species.

Maximum parsimony analysis produced 468 shortest trees. Maximum likelihood analyses produced three equally likely trees, one of which is shown in Fig. 6. Both MP and ML analyses identified two clades within the in-group most similar to those of the ITS data analyses, a *B. kingii* clade including samples of *B. hamiltonii* + *B. kingii* + *B. maxwellii* and a *B. longiflora* sensu lato clade including samples of *B. collinsii* + *B. kerrii* + *B. longiflora*. The *B. kingii* sensu lato clade received 62% BS and 0.78 PP. Unlike the ITS data analyses results, the combined data analyses produced highly resolved topologies within this clade. Significantly, *B. maxwellii* is resolved as monophyletic (83% BS; 1.00 PP). *Boesenbergia hamiltonii* and *B. kingii* samples are grouped together with 51% BS and 0.95 PP. *Boesenbergia hamiltonii* was also resolved as monophyletic, but with weak support (<50% BS, 0.86 PP). The *B. longiflora* sensu lato clade was strongly supported (95% BS; 1.00 PP) with significant internal structure and support. *Boesenbergia collinsii* was supported as monophyletic (100% BS; 1.00 PP) as was *B. kerrii* (93% BS, 1.00 PP). The single sample of *B. longiflora* was sister to *B. kerrii* (64% BS, 0.64 PP), but this placement should be viewed with caution.

Multiple accessions for each taxon (except *B. longiflora*) were included to assess genetic variation within and among the newly identified taxa. The amount of sequence variation within each taxonomic clade was generally less than the amount of variation between clades as is shown by the phylograms in Figs. 4–6. Despite the higher level of sequence diversity within *B. kingii*, it is supported as monophyletic. The results of both maximum parsimony and maximum likelihood analyses of DNA data presented above consistently identified five mostly strongly supported clades within the *B. longiflora* complex: *B. collinsii*, *B. hamiltonii*, *B. kerrii*, *B. kingii* and *B. maxwellii*. The data also support two sister relationships, one between *B. collinsii* and *B. kerrii*, and one between *B. hamiltonii* and *B. kingii*. The position of *B. longiflora* and *B. maxwellii* are less clear. The relationship of *B. longiflora* to these taxa is uncertain due to polymorphism in the nuclear (ITS) data set, but it is clearly closely related to them. *Boesenbergia maxwellii* jumps between the two clades depending upon data set examined. Finally, additional data are needed to test between various hypotheses (incomplete concerted evolution due to genetic drift post polyploidisation, hybridisation, or incomplete lineage sorting) to explain the high level of genetic variation detected in the nrITS of *B. kingii*. Overall, although there are a number of questions remaining, the molecular data allowed for the delineation of six taxa.



**Fig. 6.** Single best Maximum Likelihood phylogram ( $-\ln=5747.386$ ) for *B. longiflora* and closely related taxa based on analysis of combined chloroplast *trnK* intron and nuclear ribosomal ITS data. Support values (Bootstrap/Posterior Probability) for critical branches are show above branches. Numbers in bold typeface indicate strong support.

## Taxonomy

A field key to the *Boesenbergia longiflora* clade of species as elucidated above is provided here (see also Table 1.)

### Key to six species in the *Boesenbergia longiflora* alliance

- 1a. Flowers light yellow to bright, darker yellow ..... 2
- b. Flowers pure white to creamy white ..... 4
- 2a. Plants c. 50–80 cm., leaves broad, some horizontal, thecae red (Thailand) ..... *B. collinsii*
- b. Plants 1–1.2 m tall, leaves narrower, more vertical ..... 3
- 3a. Flowers small, c. 2.5–3.0 cm, very saccate, staminodes light yellow, throat red maculate, labellum medium yellow, apex entire, thecae white (Burma) ..... *B. longiflora*
- b. Flowers larger, c. 3.5–4.0 cm, saccate, staminodes very light yellow to white, throat red-orange, maculate, labellum streaked with red, apex truncate, thecae light yellow (W Thailand) ..... *B. kerrii*
- 4a. Rhizomes many, running, cylindrical, c. 5–15 mm diameter, flowers white to creamy white, throat red, sometimes with pink apex (NE India, Burma, SW China, Thailand) ..... *B. kingii*
- b. Rhizomes few, small, with vertical tuberous roots c. 16 cm long ..... 5
- 5a. Labellum apex light pink, throat red (NE India) ..... *B. hamiltonii*
- b. Labellum light and dark pink, throat orange, very frilled, crisped, large flower (Burma, N Thailand, Lao P.D.R.) ..... *B. maxwellii*

### Enumeration of species

***Boesenbergia longiflora*** (Wall.) Kuntze, Revis. Gen. Pl. 2: 685 (1891). – *Gastrochilus longiflorus* Wall., Pl. Asiat. Rar. 1: 22, t. 25 (1829) (“*longiflora*”). – *Curcumorpha longiflora* (Wall.) A.S.Rao & D.M.Verma, Bull. Bot. Surv. India 13: 339 (1974), pro comb. LECTOTYPE (designated here): *Wallich 6589A* (K, IDC microfiche 7394, digital image seen) Burma, Rangoon. (Fig. 1, 7, 17 & 19A).

**Deciduous herb** up to 1 m tall; **rhizome** small, irregularly shaped, c. 1 cm diam., externally brown, internally light yellow to white; multiple, small bulb-like rhizomes



**Fig. 7.** *Boesenbergia longiflora* (Wall.) Kuntze. **A.** First-day flower. **B.** Second-day flower. **C.** Plants. **D.** New rhizomes and tuberous roots. A–D, *M11P48*. (Photos: J. Mood)



surrounding the main rhizome, c. 1 cm long, pink or white; tuberous roots two or more, c.  $8 \times 0.5$  cm, tapering to a tuber, c.  $2 \times 1$  cm, externally white or pink, internally white, root hairs few, c. 20 mm long, thin, white. **Pseudostem** up to c. 30 cm long, composed of leaf sheaths, base c. 2–2.5 cm diam., 1–2 short leafless sheaths at the base, leaf sheaths c. 10–16 cm, longitudinally ridged, green, glabrous, margin hyaline. **Leaves** 5–8 per pseudostem; petiole 9–18 cm, deeply channelled, green, glabrous; ligule slightly bilobed, lobes an extension of the hyaline margin, 2 mm long, slightly acute, protruding outward, green, glabrous; lamina elliptical or broadly ovate, c.  $41\text{--}61 \times 20\text{--}21$  cm, plicate, ventrally dark green, glabrous, dorsally lighter green, glabrous with a few hairs on the midrib, base rounded to cordate, sometimes asymmetric, apex acute to long acuminate. **Inflorescence** radical, c. 3–4 per pseudostem, up to c. 12 cm long (including peduncle) produced from the side of the rhizome, peduncle c. 1–3 cm long, white, glabrous, basal sheaths 1–2, pink and white, glabrous; spike horn-shaped,  $5\text{--}10 \times 1\text{--}2$  cm. **Bracts** cymbiform, 3–4, c.  $5\text{--}6 \times 1.5$  cm, distichously arranged, red and green, glabrous, each bract enclosing one flower, some basal bracts sterile, apex sometimes curved; **bracteole** cylindrical, c.  $5 \times 0.5$  cm, white, translucent, glabrous, open to the base, apex acute. **Flowers** 2–3 per inflorescence, up to c. 11 cm long. **Calyx** tubular,  $20 \times 5$  mm, white, translucent, glabrous, apex bi-dentate. **Floral tube** 10 cm long, c. 3 mm wide at the base, white, glabrous externally and internally, corolla lobes (dorsal and ventral) linear to lanceolate, c.  $2 \times 0.5$  cm, yellowish-white, glabrous, margins involute; androecial tube cup-shaped, c. 4–5 mm long, c. 7 mm diam. at the top, yellowish-white, glabrous externally and internally. **Labellum** saccate, semi-orbicular, 2.2–2.5 cm long, 2.0–2.2 cm wide (when flattened at broadest point) light yellow, throat centre dark red, maculate with yellow showing through as dots, red pattern broadening to the lip apex, glabrous, margin wavy or wrinkled, revolute on the sides, apex elongate, emarginate; **lateral staminodes** obovate,  $1.3 \times 1.0$  cm, light yellow, glabrous, apex rounded. **Stamen** 8 mm long, filament 1 mm long, 2 mm wide at base, light yellow, few short glandular hairs, anther 7 mm long, 2 mm wide (first day) then 5 mm wide (thecae diverging on the second day) apex rounded with no anther crest, thecae c.  $7 \times 1$  mm, white, dehiscing along the entire length. **Ovary** c.  $7 \times 3$  mm, trilocular, axile placentation, white, glabrous; **style** filiform, white, glabrous, **stigma** rounded, white, ostiole transverse, without cilia, exuding a sticky liquid on the second day; **epigynous glands** linear, two, 4 mm long, light yellow. **Fruit** not seen. [Measurements based on living, cultivated material of *M11P48*, originating from *Kress 03-7305* (US)].

**Distribution.** So far known only from two locations in Burma (Fig. 20).

**Ecology.** Collected in the understorey of a primary teak forest [*Kress 03-7305* (US)]. More observations are needed in Burma to fully document the ecology.

**Phenology.** Flowering from May to September with a two-day flowering cycle for each flower.

*Etymology.* Latin, *longus* = long and *flos* = flower. Named by Wallich for the long flower.

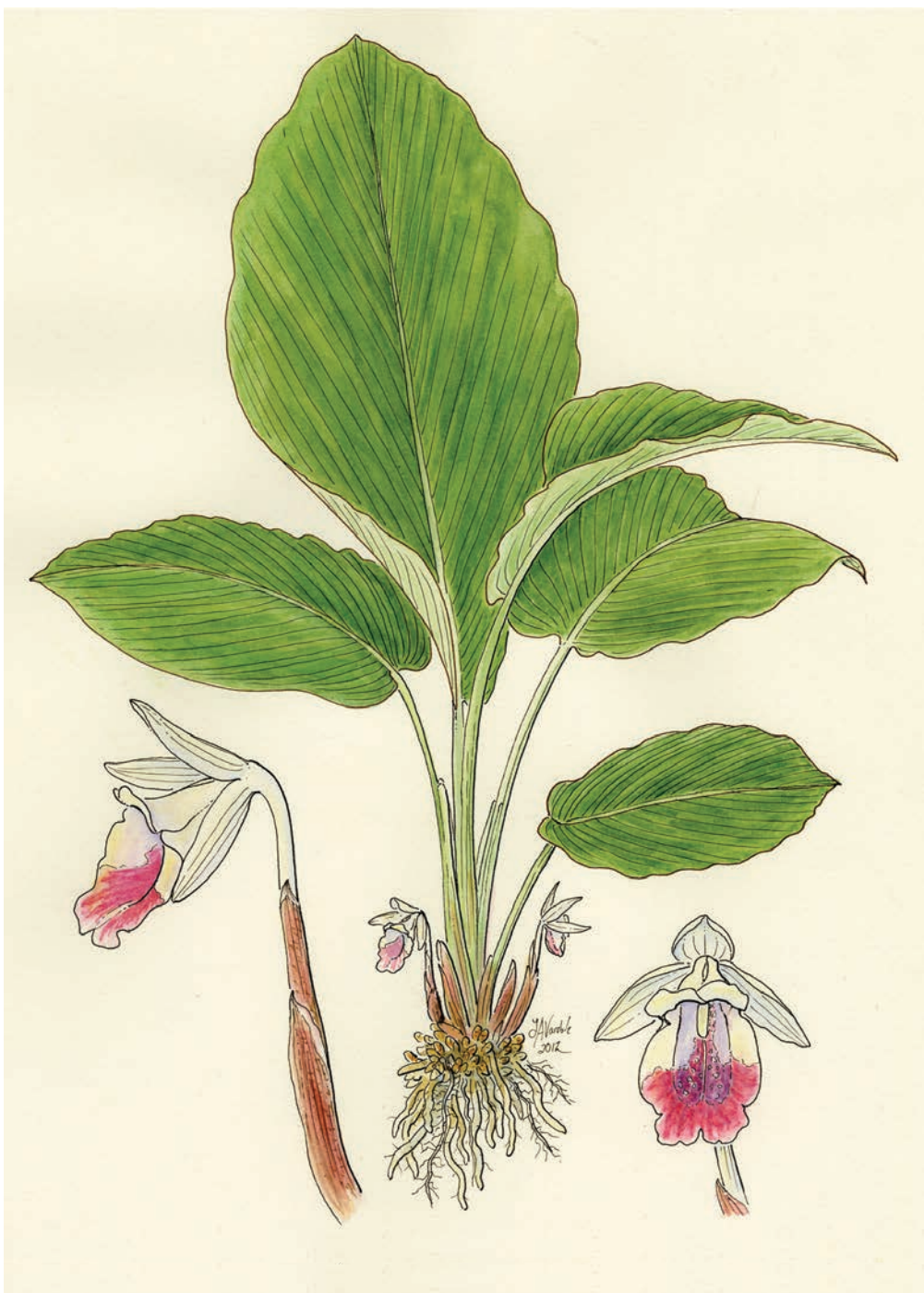
*Notes.* The cultivated material (*M11P48*) was grown from dormant rhizome divisions of *Kress GH2003-051* cultivated at the Smithsonian Institution, and originally collected on 18 June 2003, in Rakhine state, Burma as *Kress 03-7305* (US). This accession compared very well with Wallich's description and watercolour (Fig. 1). The only exception was the lack of pigmentation on the lower lamina surface, a character found to be highly variable throughout this clade. Of note are the very small, bulb-like rhizomes which develop en masse, underground, at the base of the pseudostem. Each of these small entities are loosely attached to the main rhizome and if separated can produce a new plant. *Wallich 6989B* (CAL, K, microfiche 7394) annotated and listed as *G. longiflora* (Wallich 1832) has a terminal inflorescence and as such, appears to be a different taxon, perhaps related to *B. siphonantha* (King ex Baker) M.Sabu, Prasanthk. & Škorničk.

***Boesenbergia kerrii*** Mood, L.M.Prince & Triboun, **sp. nov.**

*Boesenbergiae longiflorae* (Wall.) Kuntze *affinis, inflorescentiis 4 vel plus floribus, floribus maioribus 3.8–4.0 cm longis c. 2.8 mm latis, labello elongatiore truncato apice indentato differt.*

*TYPUS:* *Mood & Triboun 12P170*, Cultivated in Hawaii, USA, 1 Nov 2012 (holo BK; iso AAU). Originally from Thailand, Tak Province, Khao Pa Wo District, near Mae Sot, c. 600 m asl, 16°48.783'N 98°39.70'E, 8 September 2010, *Mood & Triboun 2044*, cultivated as *M2044*. (Fig. 8, 9, 17 & 19B)

***Deciduous herb*** up to 1.2 m tall; ***rhizome*** small, globular, c. 1 cm diam., externally red, pink or light tan, internally light yellow to white; multiple, small bulb-like rhizomes surrounding the main rhizome, c. 1 cm long, pink turning red with age; tuberous roots few to numerous, c. 12 × 0.5–0.8 cm, tapering to a point, externally and internally white, root hairs few, c. 10 mm long, thin, white. ***Pseudostem*** up to 30 cm, composed of leaf sheaths, base oval, c. 2–2.5 cm diam., 1–2 leafless sheaths at the base, leaf sheaths longitudinally ridged, green, glabrous, margin hyaline. ***Leaves*** 5–8 per pseudostem; petiole 9–18 cm, deeply channelled, green, glabrous; ligule slightly bilobed, lobes an extension of the hyaline margin, 2 mm long, green, glabrous; lamina elliptical or broadly ovate, c. 41–61 × 20–21 cm, plicate, ventrally dark green, glabrous, dorsally lighter green, glabrous with a few hairs on the midrib, base rounded to cordate, sometimes asymmetric, apex acute to long acuminate. ***Inflorescence*** radical, c. 3–6 or more per pseudostem, up to c. 15 cm long (including peduncle) produced from the side of the rhizome; peduncle c. 1–4 cm long, white, glabrous, basal sheaths 1–2, pink and white, pubescent; spike horn-shaped, 5–12 × 1–2 cm. ***Bracts*** cymbiform, 4–6, c. 4–5 × 1.5–2 cm, distichously arranged, green and red, glabrous, each bract enclosing one flower, some basal bracts sterile, apex sometimes curved; ***bracteole*** cylindrical, c. 5 × 0.5 cm, white, translucent, glabrous, open to the base, apex acute. ***Flowers*** 3–6



**Fig. 8.** *Boesenbergia kerrii* Mood, L.M.Prince & Triboun. Ink line drawing with watercolour of the type plant by Linda Ann Vorobik (2012).





**Fig. 9.** *Boesenbergia kerrii* Mood, L.M.Prince & Triboun. **A.** First-day flower of *M2044*. **B.** Second-day flower of *M2044*. **C.** Plants of *M2049*. **D.** Rhizomes and tuberous roots of *M2058*. **E.** Typical habitat on limestone with bamboo. (Photos: J. Mood)



per inflorescence, up to c. 15 cm long. **Calyx** tubular,  $2.0 \times 0.5$  cm, white, translucent, glabrous, apex bi-dentate. **Floral tube** 12–14 cm long, c. 3 mm wide at the base, white, glabrous; corolla lobes (dorsal and ventral) linear to lanceolate, c.  $2 \times 0.5$  cm, white to light yellow, glabrous, margins involute; androecial tube cup-shaped, c. 4–5 mm long, c. 10 mm diam. at the top, yellow, glabrous externally and internally. **Labellum** saccate, semi-orbicular, 3.8–4 cm long, 2.2 cm wide (when flattened at the broadest point) light yellow, throat centre orange-red, maculate with yellow showing through as dots, red pattern broadening toward the lip apex, ending c. 10 mm short of the apex, then dark red streaks to the apex, glabrous, margin entire, revolute on the sides, apex shortly to deeply bilobed, 2–8 mm, slightly wavy; **lateral staminodes** obovate,  $1.3 \times 1$  cm, light yellow, glabrous, apex rounded, revolute, margin wavy. **Stamen** 11 mm long, filament 2 mm long, 2 mm wide at the base, light yellow, with a few short glandular hairs, anther 9 mm long, 3 mm wide (first day) then 6 mm wide (thecae diverging on the second day) apex rounded with no anther crest, thecae c.  $9 \times 1$  mm, light yellow, dehiscing along the entire length. **Ovary** c.  $8 \times 4$  mm, trilocular, axile placentation, white, glabrous; **style** filiform, yellowish-white, glabrous, **stigma** round to oval, white, ostiole oval, without cilia, exuding a sticky liquid on the second day; **epigynous glands** linear, two, 5 mm long, light yellow. **Fruit** not seen. (Measurements based on living, cultivated material of M2044).

**Distribution.** This species is prevalent in western Thailand from the southern area of Tak Province to the southern area of Kanchanaburi Province. It should be expected in E. Burma.

**Ecology.** This species has been found only in close proximity to limestone rock outcrops. In almost all situations observed, the primary canopy component was bamboo with mixed deciduous, hardwood species. The plants grow in the cracks between limestone rocks where there is accumulation of organic matter or in deeper soils surrounding the limestone karsts. In the dry season these areas are often burnt, leaving a biochar residue. Shade is variable from light to medium. Plants commonly occur as single individuals, but over time, can create small populations of scattered plants. The result is a group of separate stems growing close together or scattered about.

**Phenology.** Flowering from June to October with a two-day flowering cycle for each flower.

**Etymology.** Named in honour of Arthur F.G. Kerr (1877–1942) one of the ‘founding fathers’ of botany in Thailand. His two specimens from the Thailand/Burma border (1922) appear to be the first collections of this new taxon.

**Additional specimens examined:** THAILAND. **Tak Province.** Umphang, Kao Hua limestone hills, 13 Jun 1922, *Kerr 6133* (P, C; \*); South of Mae Sot along Maenam Moei, 17 Jun 1922, *Kerr 6144* (K, L, P; \*); Khao Pha Wo, 23 Jul 1973, *Murata, Fukuoka & Phengkhlai T-16947* (BKF); Khao Pha Wo, 23 Jul 1973, *Murata, Fukuoka & Phengkhlai T-16949* (BKF, KYO,

L); Mae Sot Dist., 20 Aug 1994, *Maxwell 94-911* (BKF). **Kanchanaburi Province.** Tha Sao Dist., 14 Sep 2010, *Mood & Chalermglin 2049* (BISH; \*); Huai Kayeng Dist., 15 Sep 2010, *Mood & Chalermglin 2058* (BISH; \*); Sai Yok, 16 Sep 2010, *Mood & Triboun 3009* (BISH; \*); Sai Yok, 100 m, Aug 1928, *Marcan s.n.* (C, K); Ka Tha Lai, Fan Faung River Valley, 25 km east of Wangka, 1 Jun 1946, *Kostermans 787* (AAU, BO, C, L, P; \*); Sai Sok Falls, 30 Jun 1963, *Larsen 10349* (AAU; \*); Dong Yai Ban Ka Kwang, 14 Aug 1971, *Phengkhlai 2959* (AAU, BKF); Thong Pa Phum, 5 Jul 1973, *Maxwell 73-109* (AAU; \*); Sai Yok, *Marcan s.n.* (C, K); Thong Pha Phum, *Triboun 21* (BK; \*); Huay Ban Kao to Kritee, 4 Jul 1973, *Geesink & Phengkhlai 6088* (BKF, L).

*Notes.* *Boesenbergia kerrii* is similar to *B. longiflora*, but the former has a more exerted, longer floral tube, broader, longer lip with a truncate apex, different labellum colour pattern and rectangular throat opening. When habitats are compared, *B. kerrii* is found only on or around limestone, while the type of *B. longiflora* and the specimen, *Kress 03-7305* (US) appear to have been collected on sandstone or shale derived soils (USACE 1990). The small, bulb-like rhizomes described under *B. longiflora* are also found in *B. kerrii*.

***Boesenbergia collinsii* Mood & L.M.Prince, sp. nov.**

*Boesenbergiae longiflorae affinis, rhizomatium parvorum aliquot absentia radicibus longis crassis tuberosis abuntis, pseudocaulis brevioris 50–80 cm longo, floribus maioribus 4–4.2 cm longis 3 cm latis differt.*

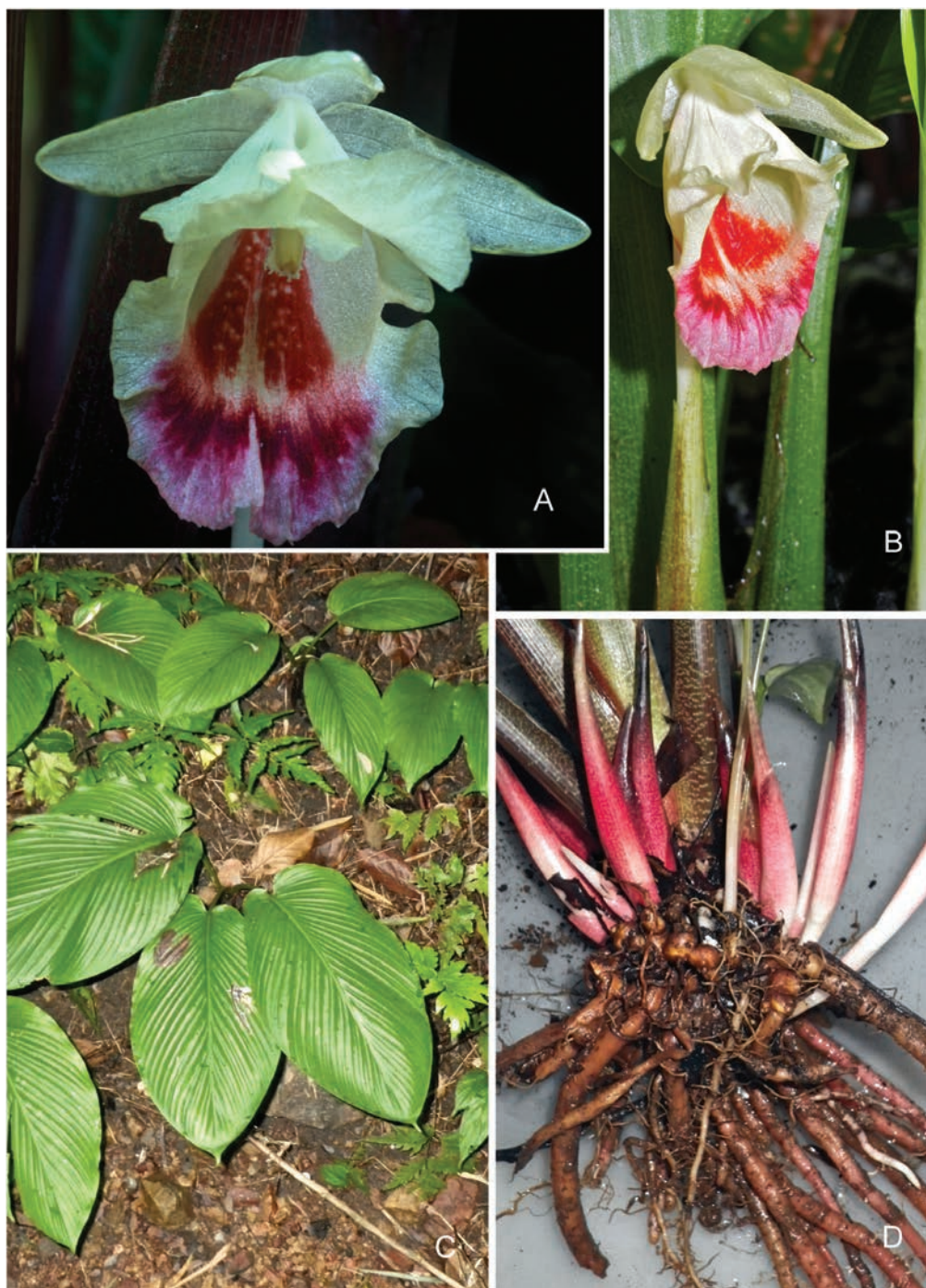
TYPUS: *Mood 12P171*, Cultivated in Hawaii, USA, 1 Nov 2012 (holo BK; iso AAU). Originally from Thailand, Loei Province, eastern border with Nong Bua Lamphu Province, along road to Udon Thani, no exact location, c. 300 m asl, August 2003, *Collins T-3068*, cultivated as *M06P14*. (Fig. 10, 11, 17 & 19C)

**Deciduous herb** up to 80 cm tall; **rhizome** small, elongate c.  $5 \times 0.5$  cm, externally brownish, internally yellow; tuberous roots prolific, c. 15–20, c.  $10 \times 1$  cm, swelling to 1.5 cm in the lower third or tapering, externally pink, internally three concentric pink rings, root hairs many, c. 8 mm long, thin, white. **Pseudostem** up to c. 20 cm long, composed of leaf sheaths, base oval, c. 2–2.5 cm diam., 1–2 leafless sheaths at the base, leaf sheaths longitudinally ridged, green or green and red, glabrous, margin hyaline. **Leaves** 5–6 per pseudostem; petiole 12–16 cm, deeply channelled, light green or reddish, glabrous; ligule slightly bilobed, lobes an extension of the hyaline margin, c. 3 mm long, white, glabrous; lamina elliptical or broadly ovate, c.  $28\text{--}44 \times 12\text{--}19$  cm, ventrally dark green, glabrous, dorsally lighter green, glabrous with a few hairs on the midrib, base rounded to cordate, sometimes asymmetric, apex acute to long acuminate. **Inflorescence** radical, c. 3–6 or more per pseudostem, up to c. 9 cm long (including peduncle) produced from the rhizome below the stem; peduncle c. 1 cm long, white, glabrous, basal sheaths 1–2, white, glabrous; spike horn-shaped,  $5\text{--}8.5 \times 3$  cm. **Bracts** cymbiform, c. 4, c.  $5\text{--}8 \times 1.5\text{--}2$  cm, distichously arranged, green or dark red, each bract enclosing one flower, apex sometimes curved; **bracteole** cylindrical, c.  $5 \times 0.5$  cm, white, translucent, glabrous, open to the base, apex acute. **Flowers** c. 4 per inflorescence, up to c. 15 cm long. **Calyx** tubular,  $2 \times 0.5$  cm, white, translucent,



**Fig. 10.** *Boesenbergia collinsii* Mood & L.M.Prince. Ink line drawing with watercolour of the type plant by Linda Ann Vorobik (2012).





**Fig. 11.** *Boesenbergia collinsii* Mood & L.M.Prince. **A.** First-day flower of *M06P14*. **B.** & **C.** Flower and plants of *M3035*. **D.** Rhizome and tuberous roots of *M06P14*. (Photos: J. Mood)



glabrous, apex bi-dentate. **Floral tube** 14 cm long, 3 mm wide at the base, white, glabrous externally and internally, dorsal corolla lobe lanceolate,  $3\text{--}3.2 \times 1$  cm, creamy white, glabrous, margins involute, ventral lobes linear,  $4 \times 0.6$  cm, creamy white, glabrous, margins involute; androecial tube cup-shaped, c. 8 mm long, c. 5 mm diam. at the top, yellow, glabrous externally and internally. **Labellum** saccate, semi-orbicular, 4–4.2 cm long, 3 cm wide (when flattened at broadest point) light yellow, throat centre bright orange-red, maculate with yellow showing through as dots, interrupted with a yellow, irregular band, then a dark red band across the lip, turning to pink towards the apex, externally with a few glandular hairs, internally glabrous, margin entire, revolute on the sides, apex slightly truncate, wavy; **lateral staminodes** obovate,  $1.6 \times 1$  cm, light yellow, dorsal surface with few glandular hairs, ventral surface glabrous, apex rounded, revolute, margin wavy. **Stamen** 11 mm long, filament 1.5–2 mm long, 2–3 mm wide at the base, light yellow, few glandular hairs, anther c. 9 mm long, 3 mm wide (first day) then c. 6 mm wide (thecae diverging on the second day) apex slightly bilobed with no anther crest, thecae  $9 \times 1$  mm, red, dehiscing along the entire length. **Ovary** c.  $8 \times 5$  mm, trilocular, axile placentation, white, glabrous; **style** filiform, white, glabrous, **stigma** rounded to oval, white, ostiole oval, without cilia, exuding a sticky liquid on the second day; **epigynous glands** narrowly ovate, two, 5 mm long, light yellow. **Fruit** a capsule, elliptical, c. 2 cm long, 1 cm wide, trilocular, white, glabrous, dehiscence loculicidal, valves rolling outward into coils; seed round, c. 15, c. 3 mm diam., light brown, slightly pubescent, aril white, translucent. (Measurements based on living, cultivated material of M06P14).

**Distribution.** This species is more northerly in distribution than *B. kerrii*, extending from Northern Lampang Province into Southern Lamphun Province. Moving eastward, the species is not documented again until the mountains of northern Phitsanulok Province, then northward into Loei and Nong Bua Lamphu Provinces. Currently, there are no known specimens from the Lao P.D.R.

**Ecology.** This species has been found only on or around the base and slopes of limestone outcrops in secondary forest with bamboo. Specimens from eastern Thailand also occur on the lower slopes of larger mountains with limestone geology. The plants prefer wet, but well-drained micro-habitats, even growing in the cracks and crevices of rock similar to *B. kerrii*. A single plant was found growing in a tree crotch, possibly indicating some consumption of the capsules and seed by rodents or birds. Plants can occur singly or as small populations of scattered individuals.

**Phenology.** Flowering from June to mid-October with a two-day flowering cycle for each flower.

**Etymology.** Named for Mark Collins (1963–2011) an American horticulturist who was an avid plant collector and enthusiast. For over twenty years he promoted Zingiberales worldwide and provided hundreds of plants to botanical gardens for conservation. This

new species was one of the numerous collections Collins brought to the attention of the first author over many years of cooperation.

*Additional specimens examined:* THAILAND. **Lamphun Province.** Li District, 4 Sep 2010, *Mood & Triboun 2010* (BISH; \*); Li District, 5 Sep 2010, *Mood & Triboun 2011* (BISH; \*). **Lampang Province.** Wang Tong District, 12 Aug 1998, *Mood & Pedersen 1455* (C; \*); Wang Nua, 28 Jun 1996, *Maxwell 96-927* (BKF, CMU, L). **Phitsanulok Province.** Tung Salaeng Luang, Jul 1966, *Larsen 832* (AAU, BKF; \*). **Phetchabun Province.** Pa Prack, Nam Naw, 19 Jun 1964, *Chantanamuck 789* (BKF). **Loei Province.** Phu Luang, 18 Sep 1963, *Phusomsaeng & Bunchuai 47* (BKF); Loei, *Triboun 1424* (BKF; \*). **Nong Bua Lam Phu Province.** Suwannakuha District, Ban Chokchai, 16 Aug 2011, *Mood & McMakin 3035* (BISH; \*). **Chaiyaphum Province.** Thung Lui Lai, 27 Jul 1999, *Newman 934* (BKF, E; \*). **Khon Kaen Province.** Pha Nok, Khao, 9 Sep 1963, *Smitinand 1123* (AAU; \*).

*Notes.* *Boesenbergia collinsii* is similar to *B. kerrii*, but the former has a smaller stature with broader lamina that tend to become horizontal when mature. The flower of *B. collinsii* is also larger and longer with more varied coloration and pattern. The plant normally lacks the many bulb-like rhizomes at the base of the pseudostem found in *B. kerrii* and *B. longiflora*.

***Boesenbergia maxwellii* Mood, L.M.Prince & Triboun, sp. nov.**

*Boesenbergiae longiflorae* (Wall.) Kuntze *affinis, floribus maioribus 4.5 cm longis 2.7–3.0 cm latis, labello elongato minus saccato albo demum lutescenti maculis rubris roseis vel violaceis differt.*

TYPUS: *Mood & Triboun 12P172*, Cultivated in Hawaii, USA, 1 Nov 2012 (holo BK; iso AAU). Originally from Thailand, Tak Province, Mae Lamung, secondary forest, granitic soil, c. 750 m asl, 15°48.085'N 98°53.754'E, 9 July 2010, *Mood & Triboun 2032*, cultivated as *M2032*. (Fig. 12, 13, 18 & 19D)

**Deciduous herb** up to 1.5 m tall; **rhizome** small, globular to elongated, c. 1–2 cm diam., externally yellow, internally light violet, numerous cylindrical, tuberous roots extending from the rhizome base, c. 10–20 × 0.5–0.8 cm, tapering, then enlarging into a tuber, c. 2 × 3 cm, externally white, internally pink, translucent, root hairs c. 18 mm long, thin, white. **Pseudostem** up to c. 30 cm, composed of leaf sheaths, base oval, c. 2–3 cm diam., several leafless sheaths at the base, sheaths longitudinally ridged, externally green, glabrous, internally yellow (core) margin hyaline. **Leaves** 4–6 per pseudostem; petiole c. 5–30 cm, channelled, light green, glabrous; ligule slightly bilobed, c. 2 mm long, lobes an extension of the hyaline margin, acute, green, glabrous; lamina elliptic, c. 33–50 × 15–25 cm, ventrally dark green, glabrous, dorsally lighter green, glabrous with a few hairs on the midrib, base rounded to cordate, apex acute. **Inflorescence** radical, c. 3–10 per pseudostem, up to 15 cm long (including peduncle) produced from the rhizome below the stem, peduncle 3–5 × 0.5–8 cm, white, glabrous, basal sheaths 1–2, white or pink, glabrous; spike horn-shaped, c. 8–10 × 2 cm. **Bracts** cymbiform, 5–7, c. 5–8.5 × 2–3 cm, distichously arranged, white and pink or red, translucent,



**Fig. 12.** *Boesenbergia maxwellii* Mood, L.M.Prince & Triboun. Ink line drawing with watercolour of the type plant by Linda Ann Vorobik (2012).





**Fig. 13.** *Boesenbergia maxwellii* Mood, L.M.Prince & Triboun. **A.** First-day flower of M2032. **B.** Flowers of M2032. **C.** Flowers of M11P124. **D.** Flower of M11P26 from the Lao P.D.R. **E.** Flowers, Chin State, Burma. **F.** Rhizome and tuberous roots of M2040. (Photos: A–D & F, J. Mood; E, H. Funakoshi)



glabrous, each bract enclosing one flower, apex attenuate; **bracteole** cymbiform, c. 4 × 0.5 cm, white, translucent, glabrous, open to the base, apex 2-dentate. **Flowers** 5–7 per inflorescence, up to c. 16 cm long. **Calyx** tubular, 3 × 0.5 cm, white, translucent, glabrous, apex tri-dentate. **Floral tube** c. 12–14 cm long, 3 mm wide at the base, white with a pink tinge, glabrous externally and internally, dorsal corolla lobe oblong, 3.6 × 1.3 cm, white, glabrous, apex cucullate, margins involute, ventral lobes linear, c. 4.3 × 1 cm, white, glabrous, apex sometimes cucullate, margins involute; androecial tube cup-shaped, c. 10–16 mm long, c. 12 mm diam. at the top, white, glabrous externally and internally. **Labellum** slightly saccate, elongate, 4.5–5.0 cm long, 2.7–3.0 cm wide (when flattened at the broadest point) white, throat centre orange-red, maculate with white showing through as dots, lip with an irregular, dark pink band, followed with a lighter pink and white band to the apex, abaxial surface with few glandular hairs, lip surface crinkled, margins crisped, apex entire, irregular; **lateral staminodes** obovate, c. 2.3 × 1 cm, white, abaxial surface with few glandular hairs, margins irregular, apex revolute. **Stamen** 12 mm long, filament c. 3 mm long, c. 2 mm wide at base, white, few glandular hairs, anther 10 mm long, 3 mm wide (first day) then c. 6 mm wide (thecae diverging on the second day) apex slightly bilobed, with no anther crest, thecae 10 × 1 mm, white, dehiscing along the entire length. **Ovary** c. 7 × 3 mm, trilocular, axile placentation, white, glabrous; **style** filiform, white, glabrous, **stigma** round, white, ostiole round, without cilia, exuding a sticky liquid on the second day; **epigynous glands** linear, two, 6 mm long, tan. **Fruit** a capsule, cylindrical, slightly ridged, c. 2 × 1 cm, trilocular, white, glabrous, calyx and floral tube remain partially intact, dehiscence loculicidal; seed globular, c. 3 mm diam., yellowish-brown, slightly pubescent, aril white, translucent. (Measurements based on living, cultivated material of *M2032*).

**Distribution.** This species is very common in northern Thailand. Collections from Chin State, Burma and the Lao P.D.R. are known. It might also occur in Yunnan, China.

**Ecology.** This species occurs in a variety of forest types to include evergreen, dry deciduous and mixed evergreen/deciduous. Most collections are at middle to higher elevations in mountainous terrain. Soil types vary from granitic to calcareous with high organic matter content.

**Phenology.** Flowers from June to November with a two-day flowering cycle for each flower.

**Etymology.** Named in honour of James F. Maxwell, Curator of the Chiang Mai University Herbarium, Thailand (CMU). For many years he has diligently collected, documented, identified and preserved the flora of Thailand, Burma, Cambodia and the Lao P.D.R. to include hundreds of Zingiberaceae. Several of his collections represent this new taxon.

**Additional specimens examined:** BURMA. **Chin State.** Kanpetlet, Laung Pan, Aug 2011, *Funakoshi s.n.* (MBK; \*); Kanpetlet, near Laung Pan, Aug 2011, *Funakoshi s.n.* (MBK).

LAO P.D.R. **Champasak Province**. Near Pakxong, secondary forest, 2006, 1286 m., collected by T. Wood, *Mood 11P26* (BISH; \*). THAILAND. **Mae Hong Son Province**. 6 Sep 2010, *Mood & Triboun 2017* (BISH; \*); Mae Hong Son, Khun Yuam, 5 Sep 1974, *Larsen 34174* (AAU). **Chiang Mai Province**. Dong Duat waterfalls, 4 Sep 1999, *Mood 11P124* (BISH; \*); Chiang Mai, Fang, 7 Jun 1973, *Geesink 5750* (BKF); Chiang Mai, Doi Sutep, 18 Jun 1988, *Maxwell 88-875* (BKF; \*); Chiang Mai, Sop Aep, 1 Oct 1971, *Murata T-15458* (BKF); Chiang Mai, Mae Sanam, 27 Jun 1978, *Phengkhlai 4140* (BKF); Chiang Mai, Doi Inthanon 14 Jul 1990, *Phengkhlai 7516* (BKF); Chiang Mai, Doi Inthanon NP, 20 Jul 1988, *Phengkhlai 6619* (BKF; \*); Chiang Mai, Doi Chiang Dao, 25 Sep 1971, *Murata T-14944* (AAU, BKF; \*); Chiang Mai, Doi Inthanon, 20 Jul 1988, *Tamura T-60130* (BKF); Chiang Mai, Doi Sutep, 9 Aug 1988, *Tamura T-60782* (BKF); Chiang Mai, Doi Chiang Dao, 9 Jun 1955, *Fehrain 12477* (BKF); Chiang Mai, Doi Sutep, 11 Jul 1987, *Maxwell 87-659* (BKF, CMU, L; \*); Chiang Mai, Chiang Dao, Doi Chiang Dao, 10 Jun 1989, *Maxwell 89-731* (E); Chiang Mai, Fang, 26 May 1991, *Maxwell 91-509* (E); Chiang Mai, Bo Luang, 4 Jul 1968, *Larsen 2097* (AAU, BKF, L); Chiang Mai, Doi Inthanon, 15 Sep 1995, *Larsen 46499* (AAU); Chiang Mai, Doi Chiang Dao, 11 Sep 1967, *Tagawa T-9865* (AAU); Chiang Mai, Baan Tham, Doi Chiang Dao, *Watthana 737* (AAU). **Lampang Province**. Lampang, Doi Kuhn Dahn, 27 Jun 1993, *Maxwell 93-695* (BKF, CMU, L; \*); Lampang, Jae Sawn NP, 24 Aug 1995, *Maxwell 95-575* (BKF, CMU, L). **Tak Province**. 9 Aug 2010, *Mood & Triboun 2040* (BISH; \*). **Chiang Rai Province**. Chiang Rai, Doi Yup, 13 Jun 1926, *Garrett 294* (BKF); Tha Sai, 12 Aug 1998, *Mood & Pedersen 1450* (C; \*).

*Notes.* This species is closely related to *B. kingii* as discussed in the phylogenetic analyses. Since *B. maxwellii* has a rhizome architecture different from *B. kingii*, there is little chance of misidentification where their ranges might overlap, i.e., Burma, Thailand and possibly China. The most westerly (known) record of *B. maxwellii* is in Chin State, Burma, separating it geographically from *B. hamiltonii*. *Boesenbergia maxwellii* differs from the latter in having larger flowers, different flower shape, greater labellum texture, orange throat, a light and dark pink labellum and plant size to c. 1.5 m.

***Boesenbergia kingii* Mood & L.M.Prince, sp. nov.**

*Boesenbergiae longiflorae* (Wall.) Kuntze *affinis*, *caulibus multiplicis*, *floribus maioribus* 5–6 cm *longis* 2.5–2.7 cm *latis*, *labello minus saccato elongato cremee albo fauce rubra differt.*

TYPUS: *Mood & Vatcharakorn 12P173*, Cultivated in Hawaii, USA, 1 Nov 2012 (holo BK; iso AAU). Originally from Thailand, Kanchanaburi Province, Huai Kayeng, secondary forest margin, c. 200 m asl, 14°38.49'N 98°31.40'E, 21 August 2011, *Mood & Vatcharakorn 3074*, cultivated as *M3074*. (Fig. 14, 15, 18 & 19E)

**Deciduous herb** up to c. 1 m tall; **rhizomes** numerous, horizontal runners of variable length, multiple nodes, c. 0.5–1.5 cm diam., pink or red when young, orange or red when mature, internally yellow to orange; tuberous roots few, elongate c. 6 × 0.3 cm, orange or white externally and internally, root hairs few, short, thin, white. **Pseudostems** many, up to 30 cm, composed of leaf sheaths, base oval, c. 2.5 cm diam., 1–2 short,







**Fig. 15.** *Boesenbergia kingii* Mood & L.M.Prince. **A.** Flower of M3074. **B.** Flower of M08P161. **C.** Plant habit of M3074. **D.** Inflorescence, flower and leaf of M3074. **E.** Rhizomes of M3074. **F.** Spreading habit (Assam, India). (Photos: J. Mood)



leafless sheaths at the base, leaf sheaths longitudinally ridged, cross-hatched, reddish or green, glabrous, margin hyaline. **Leaves** 3–7 per pseudostem; petiole 11–15 cm, deeply channelled, green or red, glabrous; ligule slightly bilobed, an extension of the hyaline margin, 4 mm long, white, translucent, glabrous; lamina elliptical 40–45 × 15–16 cm, ventrally dark green, glabrous, dorsally lighter green, glabrous with a few hairs on the midrib, base rounded to cordate, apex acute to attenuate. **Inflorescence** radical, c. 3–10 per pseudostem, up 18 cm long (including peduncle) produced from the top of the horizontal rhizome near the pseudostem, peduncle 1–3 × 0.5–1 cm, white or pink, glabrous, basal sheaths 1–2, 4–6 × 1.5–2 cm, white; spike cylindrical, slightly asymmetric, 11–14 × 1–1.5 cm. **Bracts** linear to cymbiform, 4–5, c. 6–11 × 1.5–2 cm, distichously arranged, white, green or red, glabrous, surface veined, each bract enclosing one flower, apex acute; **bracteole** lanceolate, c. 5–6 × 0.5 cm, white, translucent, glabrous, open to the base, apex 2-dentate. **Flowers** 4–5 per inflorescence, up to c. 20 cm long. **Calyx** tubular, 2–2.3 × 0.5 cm, white, translucent, glabrous, apex tri-dentate. **Floral tube** c. 10–15 cm long, c. 0.3–0.4 cm wide at the base, white, tinged or striped pink, glabrous externally and internally, corolla lobes (dorsal and ventral) oblong, c. 3.8–4 × 1.4 cm, creamy-white, glabrous, margins involute; androecial tube cup-shaped, c. 10–12 mm long, c. 13 mm diam. at the top, white, glabrous externally and internally. **Labellum** slightly saccate, elongate, 5–6 cm long, c. 4 cm wide (when flattened at the broadest point) white to creamy-white, throat centre bright red, maculate with white showing through as dots, lip creamy-white, abaxial surface with a few glandular hairs, margin undulate, wrinkled, apex entire; **lateral staminodes** obovate, 2.5 × 1.5 cm, creamy-white, abaxial surface with few glandular hairs, apex rounded, revolute. **Stamen** 12 mm long, filament 3–4 mm long, 2–3 mm wide at the base, white, glabrous, anther 8–9 mm long, 3 mm wide (first day) then c. 5 mm wide (thecae diverging on the second day) apex slightly bilobed with no anther crest, thecae 9 × 1 mm, white, dehiscing along the entire length. **Ovary** c. 7 × 3 mm, trilocular, axile placentation, white, glabrous; **style** filiform, white, glabrous, stigma elongate, white, ostiole vertically rectangular, without cilia, exuding a sticky liquid on the second day; **epigynous glands** narrowly ovate, two, 8 mm long, white. **Fruit** not seen. (Measurements based on living, cultivated material of M3074).

**Distribution.** A widespread species, found in Bangladesh, Burma, NE India, SW China and Thailand.

**Ecology.** The type locality is in a disturbed area on the margin of a secondary, riverine forest in very light shade at c. 200 m asl. The soil is a brown, gravelly alluvium. Recent observations of this species in Eastern Assam and Eastern Thailand were in disturbed, lowland forest with light shade. From limited observations, it seems to prefer flat terrain with loose soils having high moisture holding capacity.

**Phenology.** Flowers from May to September with a two-day flowering cycle for each flower.

*Etymology.* Named in honour of Sir George King (1840–1909) a Scottish medical doctor and botanist who worked in India starting in 1865 after graduation from medical school. For a short time he was Superintendent of the Garden at Saharanpur and Conservator of Forests in that area. From 1870–1897, he was the Superintendent of Calcutta Botanic Gardens. During the same period he became the first Director, Botanical Survey of India (Burkill 1965). His contributions to botany and science are numerous and far-reaching. The specimen *King 1020* (CAL) is the first known collection of this new species.

*Additional specimens examined.* BANGLADESH. **Chittagong Division.** Kaptai Lake, 5 Sep 1999, *Newman 980* (E; \*); Chimbuk Hill, Bandarban Hill Tracts, 8 Sep 2000, *Newman 990* (E; \*). BURMA. **Sagaing Division.** Katha Dist., Pile R.F., 20 Aug 1915, *Rogers 991* (CAL; \*); Alaungdaw Kathapa National Park, 17 Jul 1997, *Kress 97-5821* (US; \*). **Mandalay Division.** Maymyo Hills, Jun 1888, *Khan 50* (CAL; \*); Mt. Popa Park, 17 May 1996, *Kress 96-5646* (US; \*). **Shan State.** 45 miles east of Pyin-Oo-Lwin, 26 Jun 2003, *Kress 03-7366* (US; \*). CHINA. **Yunnan Province.** Xishuangbanna Prefecture (cultivated at Xishuangbanna B.G.) 1 Jul 2009, *Mood 2002* (BISH; \*); Culyun Village, 49 km SW of Simao, 12 Jul 2009, *Kress 09-8664* (US; \*). INDIA. **Sikkim.** Teesta Valley, 22 Jul 1874, *King 1020* (CAL; \*); **Assam.** Nambar Forest, 8 May, 1895, *Reporter 11375* (ASSAM; \*). THAILAND. **Phetchabun Province.** Nam Nao vicinity, 14 May 2012, *Mood & Vatcharakorn 3272* (BISH; \*).

*Notes.* The type selected here with a creamy white flower, dark red throat and white apex is the most common form observed across the range and as depicted in King's illustration (Fig. 14). Another form has also been observed with dark pink to light violet colouring on the apex similar to the colours of *B. hamiltonii*. Based on limited observations, this latter form seems to be less robust with shorter pseudostems and smaller diameter rhizomes. The multi-stemmed habit of *B. kingii* (in both forms) is the result of the rhizome morphology—running in habit with multiple growth nodes similar to a stolon (Fig. 15F). These runners grow outward from the initial plant in various directions, often producing a new pseudostem at a major node. The result can be a large, clonal population such as at the type locality, where it encompasses over 30 m<sup>2</sup> with hundreds of interconnected stems (Fig. 15C). In *ex situ* experiments a planted piece of broken rhizome produced a new mass of running rhizomes with several pseudostems after one year of growth. In this vein, a specimen from Burma, *C.G. Rogers 991* (CAL) is annotated, “Prevents the natural regeneration of Teak.” This statement can now be understood with more clarity—*B. kingii* has the potential for rapidly spreading once established in a suitable area.

***Boesenbergia hamiltonii*** Mood, S.Dey & L.M.Prince, **sp. nov.**

*Boesenbergiae longiflorae* (Wall.) Kuntze *affinis, floribus maioribus 3.5–4.5 cm longis 2.3–2.8 cm latis, labello elongato minus saccato albissimo signis rubris roseis violaceisque differt.*

TYPUS: *Dey NU53*, India, Meghalaya, Riboha District, Nongpoh, tropical, semi-evergreen forest, steep hillside along highway, c. 350 m asl, 25°57.5'N 91°51.183'E, July 2009 (holo CAL; iso ASSAM). (Fig. 2, 16, 18 & 19F)

*Gastrochilus jenkinsii* Wall. ex Voigt, Hort. Suburb. Calcutt.: 572 (1845), nom. inval., sine descr. – Voucher: *Jenkins* s.n. (CAL) India, Assam, Gowahatti. *Bangleum sulphureum* Ham., nom. nud.  $\equiv$  *Alpinia hamiltoniana* Wall., Numer. List: # 6579. 1832, nom. nud. – Voucher: *Hamilton* Ao 1808  $\equiv$  *Wallich* 6579A, India, Gualpura, 30 May 1808 (K-W).

*Gastrochilus longiflorus* auct. non Wall.: Hooker in Curtis's Bot. Mag. 69: t. 4010 (1843) (hand-coloured plate by W. Fitch; "Long-flowered Gastrochilus"); in Hook.f., Fl. Brit. India 6: 217 (1890) (= *G. jenkinsii*). – Voucher: Hooker in Curtis's Bot. Mag. 69: t. 4010 (1843).

*Curcumorpha longiflora* auct. non A.S.Rao & D.M.Verma: A.S.Rao & D.M.Verma, Bull. Bot. Surv. India 13: 339 (1974) ("1971") pro specim.

**Deciduous herb** up to 1 m tall; **rhizome** to c. 2.3 cm diam., externally yellow-brown, internally yellow; many cylindrical, tuberous roots extending from the rhizome base, c.  $12 \times 0.5$  cm, externally pink, internally white, sometimes with a swollen apex, c. 1 cm diam., 2 cm long; fibrous roots c.  $45\text{--}50 \times 0.1$  cm, yellow-white, with many secondary root hairs. **Pseudostem** up to c. 30 cm long, composed of leaf sheaths, base round to oval, c. 2.5 cm. diam., several leafless sheaths at the base, green, glabrous, leaf sheaths 12–24 cm, longitudinally ridged, lower portion reddish, upper green, glabrous. **Leaves** 3–6 per pseudostem; petiole 8–26 cm, deeply channelled, light green, glabrous; ligule, slightly bilobed, lobes an extension of the hyaline margin, 2 mm long, green or white, glabrous; lamina elliptical,  $34\text{--}44 \times 15\text{--}19$  cm, plicate, ventrally dark green, glabrous, dorsally lighter green, glabrous with a few hairs on the midrib, base rounded to cordate, apex acute. **Inflorescence** radical, c. 3–10 per pseudostem, up to c. 19 cm long (including peduncle) produced from the rhizome below the pseudostem, peduncle  $5\text{--}9 \times 0.8$  cm, white, glabrous, basal sheaths  $1\text{--}2, 3.5\text{--}4.5 \times 1\text{--}1.5$  cm, white, glabrous; spike horn-shaped,  $8\text{--}11 \times 2$  cm. **Bracts** cymbiform, 4–6, to c. 9 cm, distichously arranged, green and white, sometimes red, each bract enclosing one flower, apex sometimes curved; **bracteole** cymbiform c.  $5\text{--}6 \times 0.4$  cm, white, translucent, glabrous, open to the base, apex 2-dentate. **Flowers** 4–6 per inflorescence, up to c. 15 cm long. **Calyx** tubular,  $2\text{--}2.4 \times 0.5$  cm, white, translucent, glabrous, apex tri-dentate. **Floral tube** c. 9–12 cm long, 3–4 mm wide at the base, white tinged with pink, glabrous externally and internally, corolla lobes (dorsal and ventral) oblong, c.  $4 \times 1.2$  cm, white, glabrous, margins involute; androecial tube cup-shaped, c. 8–10 mm long, c. 12 mm diam. at the top, white, glabrous externally and internally. **Labellum** slightly saccate, elongate, 5–5.5 cm long, 3.5–4 cm wide (when flattened at the widest point) lip margins slightly crisped, crinkled, apex emarginate, white, throat centre red, maculate with white showing thru as dots, colour broadening toward the margins, ending c. 12 mm from apex, lip entirely pink to the apex, abaxial surface with few glandular hairs; **lateral staminodes** obovate,  $1.8 \times 1.5$  cm, white, abaxial surface with few glandular hairs, apex rounded to slightly acute, margins revolute in part. **Stamen** 12–14 mm long, filament 3 mm long, 3 mm wide at the base, white, glabrous, anther 10–12 mm long, 3 mm wide (first day) then c. 8 mm wide





**Fig. 16.** *Boesenbergia hamiltonii* Mood, S.Dey & L.M.Prince. **A.** First-day flower. **B.** First-day flower. **C.** Mature plant. **D.** Rhizome and tuberous roots. All photos of *Dey NU53*. (Photos: J. Mood)



(thecae diverging on the second day) apex truncate to slightly bilobed with no anther crest, thecae 10–12 × 1 mm, white, dehiscent along the entire length. **Ovary** c. 5 × 4 mm, trilocular, axile placentation, white, glabrous; **style** filiform, white, glabrous, **stigma** elongate, ostiole vertically rectangular, without cilia, exuding a sticky liquid on the second day; **epigynous glands** narrowly ovate, two, 5 mm long, tan-white. **Fruit** a capsule, cylindrical, asymmetrical, 2 cm long, 1 cm wide, calyx and floral tube remain partially intact, white, glabrous, surface smooth; seed globular, slightly flattened, apex rounded, tan-yellow, aril sparse, white, translucent. (Measurements based on living, wild material at the type location in India of *Dey NU53*).

**Distribution.** This taxon has been recorded primarily in Meghalaya and hill areas of Assam. Its full range has not been determined.

**Ecology.** This species is normally found in sloped habitats where there is some shade, good soil moisture and excellent drainage. Most plants are seen along roadside banks on forest margins or more rarely in open forests. Observed elevations range up to 500 m asl, although Rao & Verma (1974) reported elevations up to 1850 m asl. The type specimen was found growing under light shade in deep, black, well drained soil on the margin of a disturbed secondary forest at 350 m asl. Associated plants were *Shorea robusta* C.F.Gaertn., *Tectona grandis* L.f., *Musa* species, bamboo and understory herbs.

**Phenology.** Flowers from May to September with a two-day flowering cycle for each flower.

**Etymology.** Named for Francis Buchanan Hamilton (1762–1829) a Scottish surgeon and botanist in the employ of the East India Company from 1794–1815. His botanical research, collections, geographic documentation and statistical surveys provided a solid foundation for future explorers and botanists in Northeast India, Burma and Nepal. He served as Superintendent, Calcutta Botanical Gardens between 1814–1815. His two specimens of *Bangleum sulphureum* from 1808 appear to be the first collections of this new taxon.

**Additional specimens examined:** BANGLADESH: **Sylhet Division.** Laour, Jun 1830, Gomez in Wallich 6579B (K-W; \*). INDIA. **Assam.** Camrupa, 21 Jul 1808, Hamilton 12 (E; \*); Goalpara, Hamilton s.n. (Wallich 6579A, K-W, CAL); no location, no date Jenkins s.n. (ASSAM); Kamrup Dist., 13 Jun 1964, Rao 3879I (ASSAM; \*); Darrang, Batasipur, 12 May 1947, Srinivasan 2241I (ASSAM); Tangla, 24 May 1958, Nath 13387 (ASSAM); Sibsagar, Panbari, 15 Jun 1963, Deb 34846 (ASSAM). **Meghalaya.** Nongpoh, 31 Jun 1964, Joseph 37477 (ASSAM; \*); Nowgong Dist., 18 Aug 1964, Balakrishnan 39222 (ASSAM); Nowgong Dist., 31 Aug 1938, De 20327 (ASSAM); Nowgong Dist., 25 Aug 1964, Balakrishnan 39415 (ASSAM); Khasia Hills, J.D. Hooker s.n. (ASSAM, C; \*); Garo Hills, 6 Sep 1962, Deb 29216 (ASSAM); Khasia & Juanita Hills, 4 Jul 1938, De 20326 (ASSAM); Khasia & Juanita Hills, 8 Jun 1939, Deka 19668 (ASSAM); Khasia & Juanita Hills, 4 Jul 1940, Deka 20236A (ASSAM); Khasia & Juanita Hills, 23 Jun 1941, De 21089 (ASSAM; \*).

*Notes.* This species is distinguished from *B. kingii* by the small, short rhizome with long, vertical tuberous roots which usually produces only a single, robust pseudostem (Fig. 16D). Indicative of this below-ground morphology, *B. hamiltonii* is easily recognized in the field by the widely scattered, individual plants, occurring in a low-density population of seeded individuals (Fig. 16C). In contrast, *B. kingii* occurs in multi-stemmed, high-density populations of clonal and seeded individuals (Fig. 15C, F).



**Fig. 17A & B.** Flowers. Left: *Boesenbergia collinsii* (M3035); Centre: *B. kerrii* (M2044); Right: *B. longiflora* (M11P48). (Photos: J. Mood)



The flower colour of *B. hamiltonii* is pure white with a red, maculate throat and a pale pink lip apex. Colour variations between populations are primarily in degree of pigmentation. When the labellum is dissected and flattened, it is very similar in shape to *B. kingii*, but in living plants the full open, frontal shape is oval in the former and truncate or rounded in the latter. As a historical note, after Hamilton collected his two (*Banglium*) specimens in 1808, he used “*sulphureum*” (light yellow) as the specific



**Fig. 18A & B.** Flowers. Left: *Boesenbergia maxwellii* (M11P124); Centre: *B. kingii* (M11P77) Right: *B. hamiltonii* (M3209). (Photos: J. Mood)

epithet. Initially, this was a confusing issue, since no yellow flowered *Boesenbergia* had been described from NE India. Later, this anomaly was understood after examining the newly pressed flowers of all of the specimens used in this study. No matter what the original living flower colour, all turned a light yellow after drying. It appears Hamilton based his species descriptor on the dried flower colour rather than on fresh flowers. This yellow coloration can still be seen on *Hamilton 12* (E).

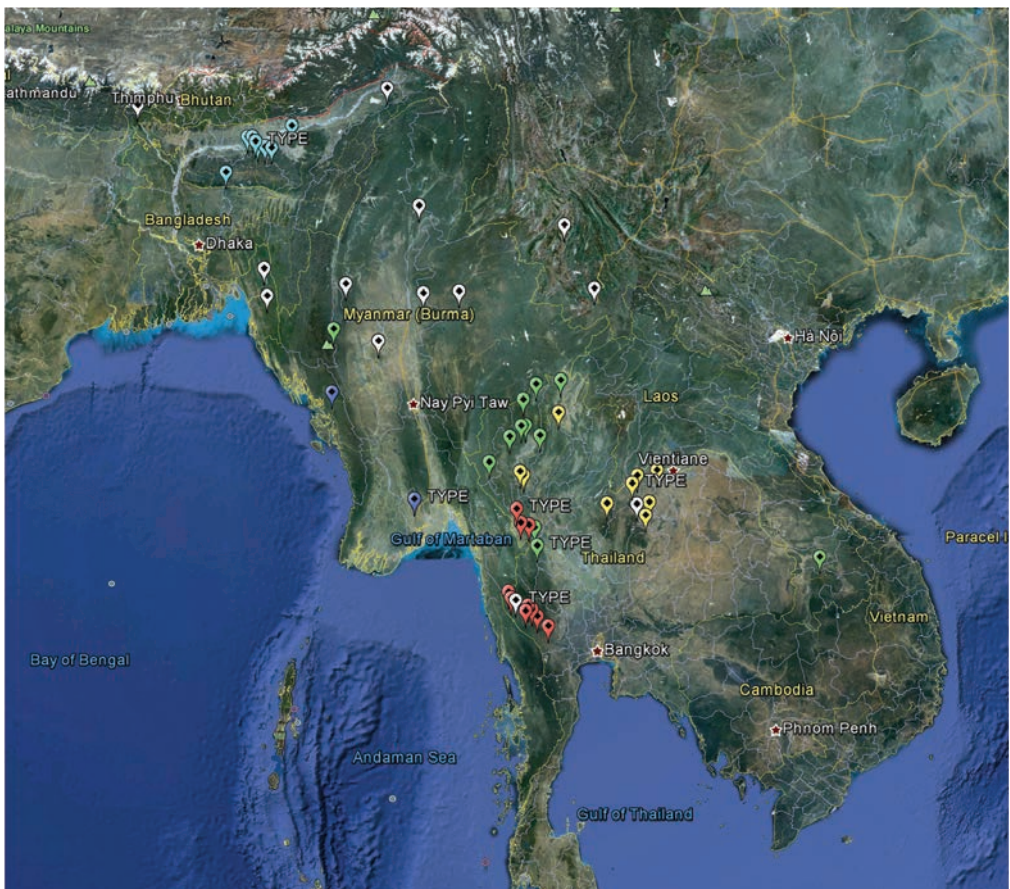


**Fig. 19.** Stamens & labellum. **A.** *Boesenbergia longiflora* (M11P48). **B.** *B. kerrii* (M2044). **C.** *B. collinsii* (M3035). **D.** *B. maxwellii* (M11P124). **E.** *B. kingii* (M11P77). **F.** *B. hamiltonii* (M3209). (Photos: J. Mood)



## Conclusions and further research

Our study fully supports Larsen's (1997) conclusion that *Curcumorpha* should be reduced to *Boesenbergia*. This is based on the phylogenetic analyses showing the *B. longiflora* clade nested within the larger *Boesenbergia* clade (Fig. 3). In further support, three of the four characters Rao & Verma (1974) used to justify *Curcumorpha* have been found to occur in other *Boesenbergia* species. Their fourth character, spiral bract arrangement, was misinterpreted and bracts are in fact distichously inserted in taxa throughout the *B. longiflora* clade. Some of their cited specimens are now determined as *B. hamiltonii*.



**Fig. 20.** Geographical distribution of the *Boesenbergia longiflora* clade showing type localities. *B. collinsii* (yellow), *B. hamiltonii* (light blue), *B. kerrii* (red), *B. kingii* (white), *B. longiflora* (dark blue) and *B. maxwellii* (green). Each specimen mapped is noted by an asterisk following the herbarium abbreviation under the “Additional specimens examined”. (Mapped in GOOGLE earth, US Dept of State Geographer, 2013 Cnes/Spot image, 2013 Mapabc.com and 2013 Google).

**Table 1.** Comparison of six *Boesenbergia* species from the *B. longiflora* clade. All measurements are derived from living material. Floral tube length = apex of ovary to base of corolla lobes; androecial tube length = base of corolla lobes to androecial tube apex (point of divergence of staminalodes, filament and labellum).

Character	<i>B. longiflora</i>	<i>B. kerrii</i>	<i>B. collinsii</i>	<i>B. maxwellii</i>	<i>B. kingii</i>	<i>B. hamiltonii</i>
Flowers per inflorescence	2–3	3–6	4	5–7	3–4	5–9 (11)
Flower colour	medium yellow	light yellow	light, dark or creamy yellow	pure white	pure white or creamy white, ageing light yellow	white
Labellum pattern colour	red throat broadening to apex	orange-red throat, dark red streaked pattern to apex	red throat with dark red and pink	orange throat with red, pink or violet combinations	red throat, with white or dark pink	red throat with uniform pink
Labellum shape	very saccate, short	saccate	saccate	slightly saccate, elongate	slightly saccate, elongate	slightly saccate, elongate
Labellum (L × W)	2.2–2.5 × 2.0–2.2 cm	3.8–4 × 2.2 cm	4–4.2 × 3 cm	4.5–5.0 × 2.7–3.0 cm	5–6 × 2.5–2.7 cm	5–5.5 × 4–4.5 cm
Floral tube length	10 cm	12–14 cm	14 cm	12–14 cm	10–15 cm	9–12 cm
Androecial tube length	4–5 mm	4–5 mm	8 mm	10–16 mm	10–12 mm	8–10 mm
Anther length	7 mm	9 mm	9 mm	10 mm	8–9 mm	10–12 mm
Underground architecture	rhizome small; few vertical tuberos roots	rhizome small; few vertical tuberos roots	rhizome small; many thick vertical tuberos roots	rhizome small; long vertical tuberos roots	many running rhizomes, 0.5–1.5 cm diameter	rhizome small; long, vertical tuberos roots

Taxa in the *B. longiflora* clade can generally be distinguished from other *Boesenbergia* by a combination of characters: robust plants with few leaves, radical inflorescences with distichous bracts and large, two-day flowers. Their annual life cycle begins as seed, rhizome-like bulbs (*B. kerrii*, *B. longiflora*) pieces of running rhizome (*B. kingii*) or mature rhizomes from the previous year. Growth begins in April or later, coinciding with the monsoon rains and continues through October when the weather becomes cooler and dry. All species are dormant for about five months. Plants of *B. maxwellii* grown in a different climate (Hawaii) with rainfall throughout the dormancy period still follow their monsoonal cycle even after 20 years of cultivation (Mood, pers. obs.).

Running rhizomes are found on all current *B. kingii* collections, including the putative hybrids. This character, at least in part, might account for its very wide distribution, whereas the other five species which propagate primarily through seed dispersal have a much smaller range.

Specimens or pictures identified as *B. longiflora* in publications prior to this study should be re-determined. For instance, the plants studied by Gao et al. (2004) are not *B. longiflora*, but appear to represent *B. kingii*. Similarly, in Larsen & Larsen (2006), the *Boesenbergia* pictured on page 32 is *B. maxwellii*, while the yellow-flowered taxon on page 48 appears to be *B. collinsii*.

Long-term observation of cultivated gingers combined with field visits to document ecology, geology, distribution, pollination biology and other elements has shown to be an excellent strategy for the study of *Boesenbergia*. The daily observation of multiple collections of various taxa from initial growth to dormancy provided insight well beyond that of field observations alone.

The current study represents a small segment of an on-going research project whose goal is to improve the overall knowledge of *Boesenbergia* by re-examining nomenclature, improving descriptions, analysing genetic relationships and providing phytochemical profiles. Additionally, further investigation of the *B. longiflora* clade continues to include karyotyping, phenology, biogeography and conservation status.

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#### Appendix A. Botanical history of *Boesenbergia longiflora*.

- 1808: Hamilton collected two ginger specimens in Assam, India which he labelled *Bangleum sulphureum* [Hamilton 12 (E) and Hamilton s.n. (Wallich 6579A, K-W, IDC microfiche 7394)].



- 1825: D. Don published *Gastrochilus* D. Don (Orchidaceae).
- 1829: Wallich published *Gastrochilus* Wall. (Zingiberaceae) with two species, *G. pulcherrima* Wall. (Wallich 6588, IDC microfiche 7394) and *G. longiflora* (Wallich 6589A, IDC microfiche 7394). The detailed descriptions were accompanied by watercolour illustrations.
- 1832: Wallich re-determined *Bangleum sulphureum* (Hamilton s.n., K-W, IDC microfiche 7394) to *Alpinia hamiltoniana* Wall. nom. nud. and identified Wallich 240 (K-W, IDC microfiche 7394) from Bengal as the same species, grouping them under Wallich 6579, A and B, consecutively.
- 1840: Wallich dispatched 51 species of living plants from the Calcutta Botanical Gardens to the Kew Gardens. On the inventory (Wallich 1840) the last two items listed are *G. pulcherrima* and *G. jenkinsii* Wall. nom. nud.
- 1842: Hooker published, “*Gastrochilus pulcherrima*. Handsome-flowered *Gastrochilus*” in Curtis’s Botanical Magazine (t. 3930).
- 1843: Hooker published “*Gastrochilus longiflora*. Long-flowered *Gastrochilus*” in Curtis’s Botanical Magazine (t. 4010). The description was accompanied by a hand-coloured plate prepared by William Hood Fitch (Fig. 2). Hooker mentioned that both *G. pulcherrima* and this species came to Kew Gardens as living plants from Wallich at the Calcutta Botanical Gardens.
- 1845: Voigt, documenting the plants at the Calcutta Botanical Gardens described the *G. longiflora* flower as “largish, pale-yellowish, with a rose-coloured lip” and mentioned that *G. jenkinsii* is from “Assam and the hills about Gowhatti. Flowered in July 1838.” Note: This places *G. jenkinsii* in cultivation at the Calcutta Botanical Gardens just prior to Wallich’s 1840 dispatch of plants to Kew Gardens.
- 1874: King collected King 1020 (CAL) in “Sikkim Himalaya.” Accompanying the specimen are two watercolour illustrations by Edward King, annotated as *G. longiflora*.
- 1890: Baker listed and briefly described six *Gastrochilus* species and three “Imperfectly known and undescribed species.” He revised part of Wallich’s original description of *G. longiflora* stating “staminodes white rather longer than the white corolla-segments lip tinged with red.” He also mentioned, “The Bot. Mag. plant is *G. jenkinsii*, Wall. mss. and has larger flowers than that figured by Wallich, of a purer white, the lip tipped with bright red.” He broadly expanded the distributional range after annotating other specimens as *G. longiflora*.
- 1891: Kuntze observed that *Gastrochilus* D. Don had priority over *Gastrochilus* Wall. and proposed *Boesenbergia* Kuntze for the later homonym.
- 1904: Schumann listed six known and three imperfectly known *Gastrochilus* species, describing *G. longiflora* as white flowered. Note: Schumann’s Fig. 13 is wrongly labelled “*Gastrochilus longiflorum*”. It is an exact copy of *G. pulcherrima*, t. 3930 (Hooker 1842).
- 1913: Schlechter accepted *Boesenbergia* Kuntze, listing 23 taxa.
- 1918: Valeton reviewed 17 Indonesian *Gastrochilus* species, commenting on the close affinity of *G. angustifolia* Hallier f. (Sumatra) to *G. longiflora*.
- 1924: Ridley listed 24 *Gastrochilus* species for the Malay Peninsula, noting *G. longiflora* only as a cultivated plant in Penang Gardens.
- 1950: Holttum provided an account of *Boesenbergia* for the Malay Peninsula, selecting *B. pulcherrima* as the type. He commented that the illustration, t. 4010 in Curtis’s Botanical Magazine (Hooker 1843) “does not agree very well with Wallich’s” and questioned

whether *B. longiflora* actually belongs to *Boesenbergia* or “may have to be transferred to another genus.”

- 1974: Rao & Verma published *Curcumorpha* A.S.Rao & D.M.Verma with a single species, *C. longiflora* (Wall.) A.S.Rao & D.M.Verma and cited 20 white-flowered specimens that reportedly differed from *Boesenbergia* by having stems spurious [a false stem] spikes radical, bracts spiral and a staminodial cup.
- 1981: Smith supported Rao & Verma’s taxonomic distinction of *B. longiflora* as *Curcumorpha* based on the four characters.
- 1997: Larsen questioned the necessity of *Curcumorpha*, suggesting that the characters mentioned by Rao & Verma were not sufficiently different from other *Boesenbergia* species and recommended that *C. longiflora* be maintained in *Boesenbergia*.
- 2002: Kress et al. commented on the phylogeny of *Boesenbergia* suggesting that *Boesenbergia* might be polyphyletic with *B. pulcherrima* allied to *Curcumorpha*.
- 2004: Gao et al. studied the floral biology of *C. longiflora* finding a two-day flowering cycle for the species.
- 2006: Sakai & Nagamasu found that a living specimen identified as *B. longiflora* (Tanaka et al. 023015, TI) had an inflorescence with a distichous bract arrangement.
- 2003–2006: Other references to *B. longiflora* or *C. longiflora* include: Vanijajiva et al. 2003, 2005; Fan 2004; Techaprasan et al. 2006; and Ngamriabsakul & Techaprasan 2006.

**Appendix B.** GenBank accession numbers (ITS/trnK) for *Boesenbergia* spp. (Zingiberaceae) used in this study. Sample number (voucher number, herbarium) GenBank numbers. Note: c=clone.

***Boesenbergia collinsii* Mood & L.M.Prince:** M06P14 (*Mood 12P171*, holotype, BK) JX992751/JX992812; MP1455 (*Mood & Pedersen 1455*, C) JX992752/JX992813; M2010 (*Mood & Triboun 2010*, BISH) JX992749/JX992810; M2011 (*Mood & Triboun 2011*, BISH) JX992750/JX992811; M3035 (*Mood & McMakin 3035*, BISH) JX992753/JX992814.

***Boesenbergia hamiltonii* Mood, S.Dey & L.M.Prince:** M3017 (*Dey NU53*, holotype, CAL) JX992754/JX992815; M3026 (*Mood 12P177*, BISH) JX992755/JX992816; M3212 (*Mood 12P178*, BISH) JX992794/no data.

***Boesenbergia kerrii* Mood, L.M.Prince & Triboun:** M2044 (*Mood & Triboun 12P170*, holotype, BK) JX992756/JX992817; M2049 (*Mood & Chalermglin 2049*, BISH) JX992757/JX992818; M2058 (*Mood 2058*, BISH) JX992758/JX992819; M3009 (*Mood & Triboun 3009*, BISH) JX992759/JX992820.

***Boesenbergia kingii* Mood & L.M.Prince:** M3074 (*Mood & Vatcharakorn 12P173*, holotype, BK) c2-JX992789, c3-JX992790, c4-JX992791, cJX992792, c8- JX992793/ JX992829; M08P161 (live material of *Kress 03-7366*, US) JX992760/JX992821; M11P47 (live material of *Kress 96-5646*, US) c1- JX992761, Cc- JX992762, c3- JX992763, c4- JX992764, c5- JX992765, c6-JX992766/ JX992822; M2002 (*Mood 2002*, BISH) c1-JX992769, c2-JX992770, c3-JX992771/JX992825; M3015 (*Mood 12P174*, BISH) c1-JX992772, c2-JX992773, c3- JX992774, c4-JX992775, c-JX992776, c12-JX992777, c13-JX992778/JX992826; M3019 (*Mood 12P175*, BISH) c1-JX992779, c3-JX992780, c6-JX992781, c8-JX992782, c9-JX992783, c10-JX992784/JX992827; M3020 (*Mood 12P176*, BISH) c7-JX992785, c8-JX992786, c9- JX992787, c12-JX992788/JX992828; M3272 (*Mood & Vatcharakorn 3272*, BISH) JX992795/ JX992830; M11P77 (live material of *Newman 980*, E) JX992767/JX992823; M11P78 (live

material of *Newman* 990, E) JX992768/JX992824; K97-5821 (*Kress* 97-5821, US) AF478742/AF478842.

***Boesenbergia longiflora* (Wall.) Kuntze:** M11P48 (live material of *Kress* 03-7305, US). c1-JX992796, c5-JX992797, c6-JX992798/ JX992831.

***Boesenbergia maxwellii* Mood, L.M.Prince & Triboun:** M2032 (*Mood & Triboun* 12P172, holotype, BK) JX992800, JX992833; MP1450 (*Mood & Pedersen* 1450, C) JX992802/JX992802; M2017 (*Mood & Triboun* 2017, BISH) JX992799/JX992832; M2040 (*Mood & Triboun* 2040, BISH) JX992801/JX992834; M11P26 (*Mood* 11P26, BISH) JX992803/JX992835; M11P124 (*Mood* 11P124, BISH) JX992804/JX992836; M11C132 (*Funakoshi* s.n., MBK) JX992805/JX992837; M11C133 (*Funakoshi* s.n., MBK) JX992806/JX992838.

***Boesenbergia plicata* var. *lurida* (Ridl.) Holttum:** M3120 (*Mood & Vatcharakorn* 3120, BISH) JX992808/JX992839.

***Boesenbergia plicata* var. *plicata* (Ridl.) Holttum:** M3177 (*Mood & Vatcharakorn* 3177, BISH) JX992807/JX992840.

***Boesenbergia pulcherrima* (Wall.) Kuntze:** M08P276 (*Mood* 08P276, BISH) JX992748/JX992809; K98-6220 (*Kress* 98-6220, US) AF478725/AF478825.



