Nomenclatural changes in Zingiberaceae: *Caulokaempferia* is a superfluous name for *Monolophus* and *Jirawongsea* is reduced to *Boesenbergia*

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ABSTRACT. Wallich published *Monolophus* Wall. (Zingiberaceae) in 1832 for two taxa he had described previously in 1820 as *Kaempferia linearis* Wall. and *K. secunda* Wall. He also mentioned *M.* ? *elegans* Wall., but the "?" indicates that he was not certain that this species belonged to this new genus. Consequently, *Monolophus elegans*, while validly published, cannot be the lectotype of the generic name. In 1964 Larsen argued against accepting *Monolophus* and established the alternative *Caulokaempferia* K.Larsen. *Caulokaempferia*, typified by the name *C. linearis* (Wall.) K.Larsen, is, however, superfluous. *Monolophus* is hereby reinstated with 22 new combinations. Its phylogenetic position is shown in relation to other genera. Based on comparative nuclear and chloroplast DNA sequence data analyses, *Jirawongsea* Picheans. (previously *Caulokaempferia*, pro parte) is reduced to *Boesenbergia* Kuntze with five new combinations.

Keywords. *Kaempferia*, molecular phylogeny, nomenclature, taxonomy

Introduction

Over the past several years the authors have been collecting molecular data from both the nuclear ITS and the chloroplast *trnK* intron to produce a phylogeny of the genus *Boesenbergia* Kuntze. In the process, other Zingiberaceae genera have been included as outgroups. *Caulokaempferia* K.Larsen is one of these genera. Until recently, this genus consisted of 29 species described from the Lao P.D.R., Northeast India and Thailand. In 2007, a molecular phylogeny of *Caulokaempferia* using samples of 23 taxa from Thailand and the Lao P.D.R. was completed (Chaiyoot, 2007). The results showed the genus to be polyphyletic with two distantly related clades. Since a sample of the type species, *Caulokaempferia linearis*, was not included, no definitive conclusion was

possible as to which clade should retain the name *Caulokaempferia*. Picheansoonthon et al. (2008) used these results in combination with the morphological characters of flower colour and capsule type (Larsen, 2003) to determine that the largest clade (18 species) represented true *Caulokaempferia*, while the smaller clade (five species) was better treated as a new genus, which was called *Jirawongsea* Picheans., despite the samples clustering within the *Boesenbergia* clade. Also, a morphological comparison of *Jirawongsea* to *Boesenbergia* was not included.

When conducting a brief historical review of *Caulokaempferia* as part of this study it was discovered that an earlier name, *Monolophus* Wallich (1832) appeared to have been validly published with two species, one of which is the type of *Caulokaempferia*. This intriguing information triggered an in-depth nomenclatural study to understand why *Monolophus* had not been used in lieu of *Caulokaempferia*.

This paper provides new insights into the nomenclature, phylogeny and morphology of *Caulokaempferia* and *Jirawongsea.*

While all four authors made significant contributions to the manuscript, JDM is the key investigator and general manager of this paper, JFV provided the historical research as a basis for nomenclatural decisions, SD was instrumental in making field observations, and LMP provided supporting molecular phylogenetic research.

Nomenclature

Wallich (1820) described two new species of *Kaempferia* L. (Zingiberaceae): *K. linearis* Wall. and *K. secunda* Wall. At the time he thought them to be atypical for this genus and gave a brief diagnosis for this "group", but not a rank, nor a name: "Caulescent, with an entire crest".

In 1829 he added *Kaempferia elegans* Wall. and stated, "[it] belongs to the section which I have long ago [1820] indicated … All three ought perhaps to be removed from *Kaempferia*, and formed into a distinct genus for which I would propose the name *Monolophus* [single, entire crest]." *Monolophus* is here a provisional name for both the section and the genus and is, therefore, invalid (McNeill et al., 2012 - Art. 36.1b) although there is, yet again, a diagnosis: "caulescent habit, absence of tubers and entire crest".

The nomenclatural articles cited here are according to the *International Code of Nomenclature* (ICN) (McNeill et al. 2012).

Wallich (1832) published *Monolophus* and included three species with references to earlier publications. Although *Monolophus* as a genus is not separately mentioned, Art. 35.1 and Ex. 1 on *Suaeda* Forssk. do not apply because the name of the genus and its three species are validly published through direct reference to previous diagnoses and descriptions (Art. 38.1). *Monolophus linearis* and *M. secunda* are clearly syntypes while *M. elegans* is not, as it was cited with a query and was not part of the original concept in 1820.

As Wallich (1829) so beautifully illustrated *Kaempferia elegans* it became the best known species of the assemblage, thus causing later problems in lectotypification (e.g. supposedly by Endlicher (1837)).

Monolophus was recognised by Endlicher (1837), followed by Steudel (1841), Horaninov (1862), Pfeiffer (1874), and more recently by Wu & Chen (1978). Endlicher's citation of *Kaempferia elegans* is not to be regarded as a lectotypification, but as a representative of the genus. As *Kaempferia elegans* is not a syntype this cannot be a lectotype, yet it was erroneously accepted by Larsen (1964: 165), followed by Burtt & Smith (1972: 216), Wu & Chen (1981), and Newman et al. (2004: 118), and thus apparently by the *Index Nominum Genericorum* (Farr, 2013).

Horaninov (1862) is sometimes cited as the validating author of *Monolophus* but from the text it is clear that he was not, as he refers to Endlicher (1837), Roxburgh (1820) and Wallich (1832).

Bentham (1883) regarded *Monolophus* as connecting *Kaempferia* L. sections *Stachyanthesis* Benth. and *Soncorus* Rumph. ex Horan. The latter is an invalid name for *Kaempferia* sect. *Kaempferia* as an autonym is required. He included only *Kaempferia linearis* and *K. secunda* and did not mention *K. elegans*.

Baker (1892) accepted *Monolophus* as a subgenus of *Kaempferia* and included seven species, some of which are now placed elsewhere, e.g. in *Boesenbergia* Kuntze, *Camptandra* Ridl., *Kaempferia* and *Stahlianthus* Kuntze. He was more or less followed by Schumann (1904: 73) who created a later isonym, as he erroneously thought that Baker had regarded it as a section.

Larsen (1964) transferred *Kaempferia linearis* and *K. secunda* to a new genus, *Caulokaempferia* with *C. linearis* as the type. This transfer was supported by then new morphological findings and cytological data.

As was argued above, Larsen (1964) was incorrect in regarding *Kaempferia elegans* as the type of *Monolophus*, which he saw as more related to *K. galanga* L., the lectotype of *Kaempferia*. He, therefore, rejected *Monolophus* because 1) the type species would be a *Kaempferia* and 2) "the name refers to a character widely distributed also in neighbouring genera". The first argument is to be rejected as *Kaempferia elegans* is not a candidate for lectotypification. The second is a taxonomic, not a nomenclatural, argument and also contravenes Art. 51.1 (a name is not to be rejected because it would be inappropriate).

Because *Kaempferia linearis* and *K. secunda* are the syntypes of *Monolophus*, Larsen (1964) created a superfluous name. The fact that, in 1964, *Monolophus* had not yet been lectotypified is irrelevant (Art. 52.2a). *Monolophus linearis* Wall. was later designated as the lectotype by Wu & Chen (1978: 28).

Even though Wu & Chen (1978) recognised the validity of *Monolophus* they later (Wu & Chen, 1981) changed their opinion on the validity of *Monolophus* and reverted to the name *Caulokaempferia* which has been in general usage to the present day.

Here we reinstate *Monolophus* as the valid name for this genus and provide 22 new combinations (Appendix 1).

Materials and Methods

Molecular phylogeny. Caulokaempferia and *Jirawongsea* leaf tissue samples were obtained from living plants (where available) and dried in silica gel. Supplemental ingroup data were obtained from GenBank, as were additional sequences which provided the scaffold for the taxa sampled here. A complete list of samples and GenBank accession numbers are provided in Appendix 4. The *Caulokaempferia* nucleotide data produced by Chaiyoot (2007) have not yet been deposited into any of the four international sequence repositories BOLD, DDBJ, EMBL, GenBank, thus they could not be included here.

DNA extraction follows Kress et al. (2002) while amplification and analytical methods follow Mood et al. (2013). Only minimal detail is provided here. The nuclear ribosomal ITS (nrITS) region was amplified using the 18S-F and 26S-R primers (Prince, 2010). The plastid *trnK* region was amplified in two parts, the first using 1F and 1235R primers and the second using mIF and 2R. Data were collected on an ABI Genetic Analyzer and sequences of each specimen were edited and a consensus sequence was generated in Sequencher v4.9 (Gene Codes Corporation, Ann Arbor, Michigan, USA). Sequences were aligned manually in Se-al (Rambaut, 1996) and areas of ambiguous alignment identified. Data were analysed under parsimony criteria by genomic data partition, firstly independently and later in combination. Data were also analysed including and excluding ambiguously aligned regions to determine if this altered the resulting tree topologies. Maximum parsimony analyses were conducted in PAUP* (version 4.0b10; Swofford, 2002). Heuristic search methods were conducted in each case with 1000 random addition replicates. Branch support was estimated using parsimony bootstrap (BS) in PAUP*.

Results

Both the individual and combined data analyses agreed in topology. All trees from all analyses agreed (or did not conflict) with a monophyletic *Caulokaempferia* (*Monolophus*) and *Boesenbergia*. Additionally, both phylogenies placed all samples of *Jirawongsea* within *Boesenbergia*. For brevity, only the results of the combined data analyses are shown and discussed below. The combined ITS and *trnK* data analysis (ambiguously aligned regions excluded) produced 64 shortest parsimony trees, one of which is shown in Figure 1. All samples of *Jirawongsea* (labelled *Boesenbergia* in Fig. 1) are part of a strongly supported (BS=100%) clade that includes *B. rotunda* (L.) Mansf. and *B. curtisii* (Baker) Schltr., which is nested within a monophyletic *Boesenbergia* (BS=56%). These findings are consistent, whether ambiguously aligned data are included or excluded from the analyses. Analyses of just the *trnK* or the ITS data partitions recover similar tree topologies. The only differences in topology generally involve minor changes in sister taxon relationships (with low support) among genera of Zingibereae. Branch support is generally lower in the separate analyses.

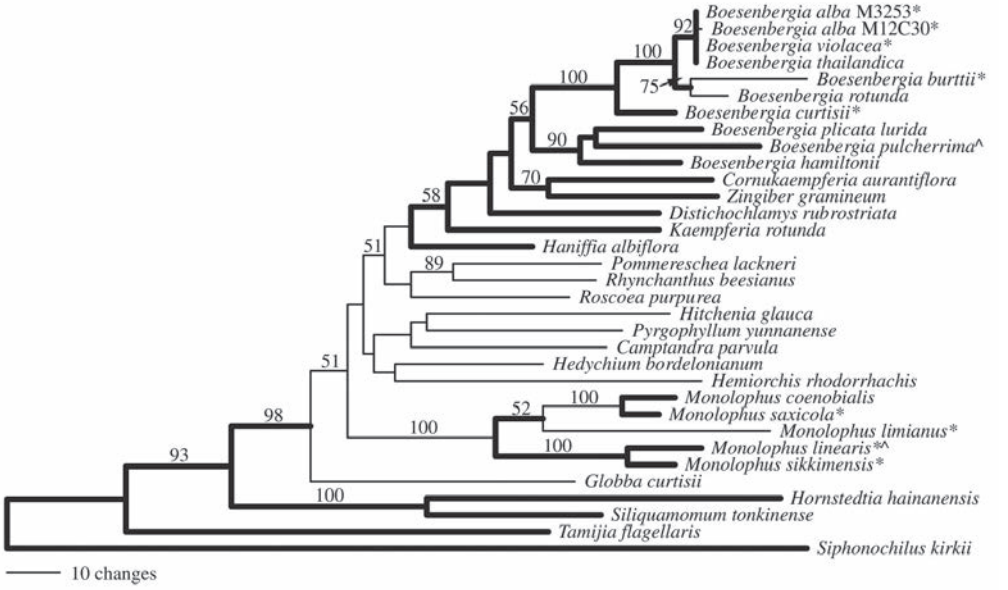

Fig. 1. Phylogram of 1 of the 64 shortest maximum parsimony trees for *Boesenbergia* and *Monolophus* (Zingiberaceae) based on an analysis of combined ITS and *trnK* sequence data. ^ indicates the type species for the genus. * indicates sequences generated for this study. Numbers above branches are bootstrap support values. Bold branches were recovered in the strict consensus tree.

Discussion

Larsen (1964) described *Caulokaempferia* with eight species that he considered to be yellow-flowered. Larsen & Smith (1972) added *Caulokaempferia alba* (white-flowered) and the yellow-flowered, *C. yunnanensis* (Gagnep.) R.M.Sm. (See Appendix 2). The inclusion of these taxa was problematic, as they were quite different from each other and the type. The authors discussed the diversity of *Caulokaempferia* and *Boesenbergia* and suggested, on balance, that these species belonged in *Caulokaempferia* but conceded that characters such as the "large concave bracts ... [with a] lamina-like extension of the apex." in *C. yunnanensis* were more complex and required extending the generic limits. Recent sampling of this taxon in molecular studies by Kress et al. (2002), Záveská et al. (2012) and here (Fig. 1), has shown it to have close affinity to *Curcuma* L., but we maintain it in *Pyrgophyllum* (Gagnep.) T.L.Wu & Z.Y.Chen. Larsen & Smith (1972) considered the flower of *Caulokaempferia alba* to be similar in appearance to other species in *Caulokaempferia*, but its vegetative form, trilocular capsule and flowering sequence required considerable accommodation. In this species the flowers open sequentially, top to bottom, whereas in the type species, they open bottom to top. Obviously, this was a disconcerting fact, as Larsen & Smith (1972) stated

"Such a mode of flowering has not been previously observed in *Caulokaempferia*, and the possibility of affinity to at least some *Boesenbergia* cannot be discarded."

Based on the first author's study of *Boesenbergia* across their range, it appears that all of the species presently described can be distinguished from all other Zingibereae (except *Haplochorema* K.Schum.) by their basipetalous flowering. This is defined here as a flowering sequence where the first flower to open is at or near the apex and subsequent flowers open sequentially down the rachis from single-flowered bracts. In contrast, *Caulokaempferia* species are acropetalous with the flower-opening sequence from bottom to top. It should be noted that some *Caulokaempferia* have circinni of 2–4 flowers per bract, and in this case, the flowering sequence in the circinni in relation to the overall sequence is undocumented.

Larsen & Smith (1972) mentioned several characters in *Caulokaempferia alba* which they thought were atypical of *Boesenbergia*—a non-saccate labellum, a crested anther and no [androecial] tube at the base of the labellum. In fact, these three characters have been documented in *Boesenbergia* descriptions (Valeton, 1918; Holttum, 1950). For example, *Boesenbergia rotunda* (Fig. 3C), a well-known ginger of ethnobotanical importance, and *B. curtisii* (Fig. 3D) have these "atypical" characters. Perhaps Larsen & Smith were referring to *Boesenbergia* species similar to the type, *B. pulcherrima* (Wall.) Kuntze, which have a saccate labellum, an uncrested anther and an androecial tube (Holttum, 1950).

Wallich (1820) did not note flower colour in the original description of *Kaempferia linearis* and nor is a colour shown in the drawing received by Kew (K) on October 17, 1828 (annotated as "Wallich 1828 East Ind. Co. #25"). The first mention of the flower colour was by Baker (1892) who noted "flowers white ... tinged with yellow at the throat", but it is unknown where this information originated. Contrary to Baker's colour description, *Parry 281* (K) from Assam (1927) was annotated "flowers yellow". Larsen (1964) cited this specimen as representative of *Caulokaempferia linearis*, but in its description he stated " [flower] tinged with yellow at the throat".

By 2003, five more *Caulokaempferia* species had been published by Larsen (1973, 2003). Two of these, *Caulokaempferia thailandica* and *C. violacea* had characters very similar to *C. alba*. It became apparent to Larsen that the accommodation of these latter taxa [and *Caulokaempferia alba*] within *Caulokaempferia* was becoming more problematic. To preclude moving these species to another genus, he taxonomically grouped them into either yellow-flowered with unilocular capsules (to include the type) or into "the whitish- to violet-flowered species" with trilocular capsules. He further stated, "Until the relationships between these groups have been satisfactorily elucidated through molecular studies, [I have] chosen to keep the two groups united in the genus *Caulokaempferia*" (Larsen, 2003).

The first phylogenetic study to sample *Caulokaempferia* was by Kress et al. (2002). Only three species from the yellow-flowered group were included. The results showed affinity to *Haniffia albiflora* K.Larsen & Mood. Ngamriabsakul et al. (2004) and Thong-a-ram et al. (2005) sampled *Caulokaempferia violacea*, showing it to be closely allied to *Boesenbergia*. Chaiyoot (2007) sampled both *Caulokaempferia* colour groups, but without the type, *C. linearis*. His results showed the genus to be comprised of

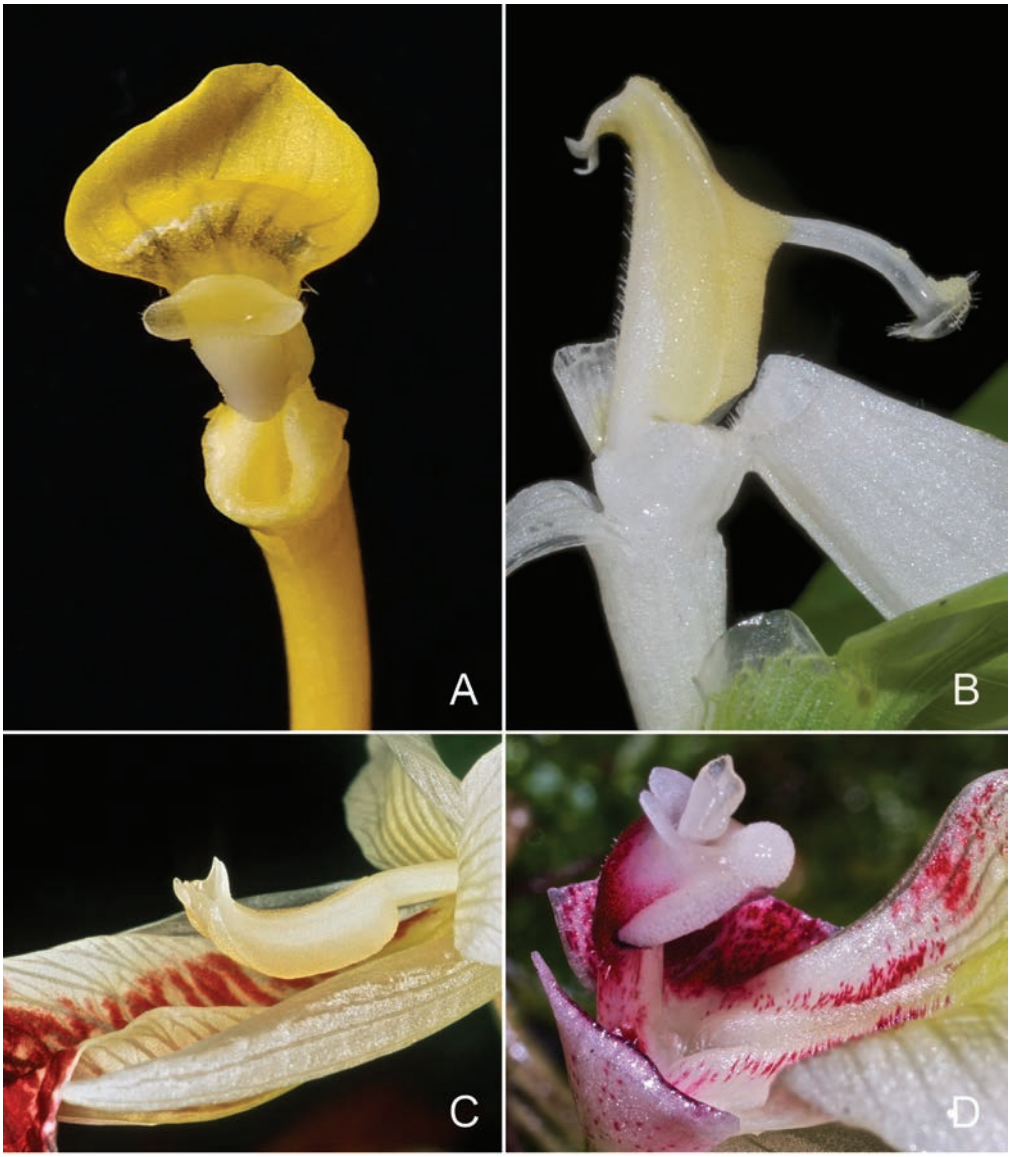

Fig. 3. A. *Monolophus petelotii* (K.Larsen) Veldk. & Mood. **B.** *Boesenbergia alba* (K.Larsen & R.M. Smith) Mood & L.M.Prince. **C.** *Boesenbergia rotunda* (L.) Mansf. **D.** *Boesenbergia curtisii* (Baker) Schltr. (Photos: A, J. Leong-Škorničková; B–D, J. Mood)

two unrelated clades. The five taxa of Larsen's white-flowered group clustered within a strongly supported monophyletic *Boesenbergia* (BS=100%). This finding brought full circle the observation of Larsen & Smith (1972) concerning the flowering sequence of *Caulokaempferia alba* being the same as in *Boesenbergia*. Picheansoonthon et al. (2008) proposed that these five taxa represented a new genus and named them *Jirawongsea*, despite the findings of the molecular data analyses. Since the type, *Caulokaempferia*

linearis had not been included by Chaiyoot (2007), no direct determination could be made as to which clade actually represented *Caulokaempferia*. In lieu of this, Picheansoonthon et al. (2008) followed the floral colour grouping of Larsen (2003) and selected the yellow-flowered group as representative of *Caulokaempferia*. To support their generic proposal, the taxonomic discussion was confined to the morphological dissimilarities between *Caulokaempferia* and *Jirawongsea* with no mention of the morphological similarities or phylogenetic affinity of the latter to *Boesenbergia*.

Figure 1 shows that *Caulokaempferia linearis* (as *Monolophus linearis*) does indeed group with the other species of *Monolophus* which are predominantly yellow-flowered. Surprisingly, as can be seen from a photograph of *Monolophus linearis* taken near the type locality in Meghalaya, India, the flower is not yellow, but white (Fig. 2B) as was stated by Baker (1892). In fact, none of the Indian species are yellow-flowered: *Caulokaempferia secunda* flowers are dark pink to violet (Fig. 2D) and those of *C. sikkimensis* are white. Consequently, taxonomic grouping by flower colour was an imperfect fit.

Based on phylogenetic and taxonomic investigations, *Jirawongsea* is reduced to *Boesenbergia* with five new combinations (Appendix 3).

Since the most recent circumscription of *Caulokaempferia* (Larsen & Smith, 1972) included characters of taxa that are no longer in this genus, an updated description of the genus is provided here under the name *Monolophus*.

Monolophus Wall., Pl. Asiat. Rar. 1: 24, t. 27 (1829), nom. prov. inval.; Wall., Numer. List 6591–6593 (1832), validation; Wall. ex Endl., Gen. Pl. 225 (1837), isonym. – *Kaempferia* L. subg. *Monolophus* (Wall.) Wall. ex Baker in Hook.f., Fl. Brit. India 6: 222 (1894); Baker ex K.Schum. in Engl., Pflanzenr. IV, 46, Heft 20: 73 (1904), isonym. – *Caulokaempferia* K.Larsen, Bot. Tidsskr. 60: 166 (1964), nom. superfl. TYPE: *Monolophus linearis* Wall., lectotype designated by Wu & Chen (1978).

Perennial herbs up to 45 cm; stems with 2–4 bladeless sheaths at the base. *Leaves* 3–10, sessile or petiolate, ligule small, bilobed to entire. *Inflorescence* terminal, acropetalous, flowers opening singly (?). *Bracts* 1–10, distichous, lanceolate, acuminate, the margins quite free to the base; 1–4 flowered. *Bracteoles* membranous, often not associated with the first flower in those species with single-flowered bracts. *Calyx* tubular, often 2–3 dentate, not deeply split unilaterally. *Floral tube* long, narrow, widening at the mouth; lobes 3, the dorsal broader and a little longer than the laterals. *Lateral staminodes* petaloid, normally small in relation to the labellum. *Labellum* large, orbicular, entire or bilobed, slightly concave. *Stamen* usually with a very short filament (occasionally up to 5 mm long) or sessile on the floral tube; anther thecae mostly parallel, dehiscing longitudinally; anther crest conspicuous, entire or dentate, often reflexed. *Epigynous glands* short, mostly linear, free from each other. *Ovary* unilocular; placentation free central. *Fruit* a unilocular capsule with a lateral suture. *Seeds* numerous, small, ellipsoid, glabrous or with a dense indumentum, aril white.

Fig. 2. A. *Boesenbergia alba* (K.Larsen & R.M. Smith) Mood & L.M.Prince. **B.** *Monolophus linearis* (Wall.) Wall. **C.** *Monolophus saxicola* (K.Larsen) Veldk. & Mood. **D.** *Monolophus secundus* (Wall.) Wall. (Photos: A & C, J. Mood; B & D, S. Dey)

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Appendix 1. Enumeration of *Monolophus* species

1. ***Monolophus amplexicaulis*** (Suksathan) Veldk. & Mood, **comb. nov.** – *Caulokaempferia amplexicaulis* Suksathan in K.Larsen et al., Nordic J. Bot. 23: 401, t. 1, 2. (2005) ("*amplexicaule*"). TYPE: Thailand, Mae Hong Son, Muang Distr., Doi Hua Kai-Doi Pui, *Wongnak et al. 705* (holotype QBG; isotypes AAU, BKF, E, K, US).

2. ***Monolophus appendiculatus*** (K.Larsen & Triboun) Veldk. & Mood, **comb. nov.** – *Caulokaempferia appendiculata* K.Larsen & Triboun in K.Larsen, Nordic J. Bot. 22: 409, t. 1 (2003). TYPE: Thailand, Chiang Mai, Ang Kang, Kop, Dung village, *Triboun 617* (holotype AAU; isotypes BK, BKF).

3. ***Monolophus bolavenensis*** (Picheans. & Koonterm) Veldk. & Mood, **comb. nov.** – *Caulokaempferia bolavenensis* Picheans. & Koonterm, in Picheans. et al, Nat. Hist. Bull. Siam Soc. 56: 86, t. 14. (2008). TYPE: Laos, Champasak, Paksong Distr., Bolaven Plateau, Tad Kamued Waterfall, *Picheansoothon & Koonterm 821* (holotype BKF; isotype SING).

4. ***Monolophus bracteatus*** (K.Larsen & S.S.Larsen) Veldk. & Mood, **comb. nov.** – *Caulokaempferia bracteata* K.Larsen & S.S.Larsen, Nordic J. Bot. 22: 411, t. 2. (2003). TYPE: Thailand, Chatuchak Market in Bangkok, originally from Nong Khai, *Larsen 47337* (holotype AAU; isotype BKF).

5. ***Monolophus chayanianus*** (Tiyaw.) Veldk. & Mood, **comb. nov.** – *Caulokaempferia chayaniana* Tiyaw., Telopea 12: 480, t. 1, 2 (2010). TYPE: Thailand, Mae Hong Son, Pai Distr., Doi Jik Jong, *Picheansoothon 1017* (holotype BKF; isotypes BK, SING).

6. ***Monolophus coenobialis*** Hance, J. Bot. 8: 75 (1870). – *Kaempferia coenobialis* (Hance) C.H.Wright, J. Linn. Soc., Bot. 36: 68 (1903). – *Caulokaempferia coenobialis* (Hance) K.Larsen, Bot. Tidsskr. 60: 177 (1964). TYPE: China, North River, Fi-loi-tsz Monastery, *Sampson 11369* (holotype K),
Roscoea flava Merr., Lingnan Sci. J. 13: 21 (1934). – Type: China, Kwangtung [Guangdong], Tsungfa-Lungmoon Distr., Sam Kok Shan, *CCC 20595* (W.T. Tsang) (holotype SYS; isotypes E, possibly in A).

7. ***Monolophus jirawongsei*** (Picheans. & Mokkamul) Veldk. & Mood, **comb. nov.** – *Caulokaempferia jirawongsei* Picheans. & Mokkamul, Folia Malaysiana 5: 75, t. 9–15 (2004). TYPE: Thailand, Nong Khai, Phu Wua, *Picheansoothon & Mokkamul 759* (holotype BKF; isotypes BK, KEP, SING).

8. ***Monolophus khaomaenensis*** (Picheans. & Mokkamul) Veldk. & Mood, **comb. nov.** – *Caulokaempferia khaomaenensis* Picheans. & Mokkamul, Folia Malaysiana 5: 6, t 2, 3B, 4– 7. (2004). TYPE: Thailand, Nakhon Si Thammarat, summit of Khao Maen, *Mokkamul 130703-01* (holotype BKF; isotypes BK, KEP, SING).

9. ***Monolophus kuapii*** (K.Larsen) Veldk. & Mood, **comb. nov.** – *Caulokaempferia kuapii* K.Larsen, Bot. Tidsskr. 60: 175, t. 5 (1964). TYPE: Thailand, Chantaburi, Mt. Khao Kuap, *Put 3016* (holotype C).

10. ***Monolophus larsenii*** (Suksathan & Triboun) Veldk. & Mood, **comb. nov.** – *Caulokaempferia larsenii* Suksathan & Triboun, Edinburgh J. Bot. 60: 513, t. 1. (2004). TYPE Thailand, Chiang Mai, Doi Phe Pan Nam, : *Suksathan, Triboun & Wongnak 3429* (holotype QBG; isotypes AAU, BK, BKF, E, K).

11. ***Monolophus limianus*** (Mokkamul & Picheans.) Veldk. & Mood, **comb. nov.** – *Caulokaempferia limiana* Mokkamul & Picheans., Folia Malaysiana 5: 188, t. 1, 2, 3, 5, 8 (2004). TYPE: Thailand, Phitsanulok ,Chat Trakan Waterfalls National Park, *Picheansoonthon & Mokkamul 742* (holotype BKF; isotypes BK, KEP, SING).

12. ***Monolophus linearis*** (Wall.) Wall., Numer. List 6592 (1832). – *Kaempferia linearis* Wall. in Roxb., Fl. Ind. 1: 20 (1820). – *Costus linearis* (Wall.) Spreng., Syst. Veg. 1: 13 (1824,

"1825"). – *Caulokaempferia linearis* (Wall.) K.Larsen, Bot. Tidsskr. 60: 170 (1964). TYPE: India, Silhet, *Gomez* ("*W.G.*") in *Wallich 6592* (holotype K; isotypes C, CAL, E, L, P, IDC microfiche 7394).

13. ***Monolophus pedemontanus*** (Triboun & K.Larsen) Veldk. & Mood, **comb. nov.** – *Caulokaempferia pedemontana* Triboun & K.Larsen in K.Larsen et al., Nordic J. Bot. 23: 403, t. 3 (2005). TYPE: Thailand, Nakon Nayok, Nang Rong Falls, *Larsen, Larsen, Tange & Niyomdham 43774* (holotype AAU; isotype BK).

14. ***Monolophus petelotii*** (K.Larsen) Veldk. & Mood, **comb. nov.** – *Caulokaempferia petelotii* K.Larsen, Bot. Tidsskr. 80: 176, t. 6. (1964). TYPE: Vietnam, Chapa, *Pételot s.n. Jul 1924* (holotype P).

15. ***Monolophus phulangkaensis*** (Picheans.) Veldk. & Mood, **comb. nov.** – *Caulokaempferia phulangkaensis* Picheans., Taiwania 53: 249, t. 3, 4, 7 (2008). TYPE: Thailand, Loei, Phu Luang, Kok Nok-kraba, *Picheansoothon 729* (holotype BKF; isotypes BK, SING).

16. ***Monolophus phuluangensis*** (Picheans. & Mokkamul) Veldk. & Mood, **comb. nov.** – *Caulokaempferia phuluangensis* Picheans. & Mokkamul, Folia Malaysiana 5: 70, t. 1, 2, 4–8 (2004). TYPE: Thailand, Loei, Phu Luang, Kok Nok-kraba, *Picheansoonthon & Mokkamul 739* (holotype BKF; isotypes BK, KEP, SING).

17. ***Monolophus phutokensis*** (Picheans.) Veldk. & Mood, **comb. nov.** – *Caulokaempferia phutokensis* Picheans, in Picheans. & Koonterm, Taiwania 53: 253, t. 5–7. (2008). TYPE: Thailand, Nong Khai, Amphoe Si Wilai, Phu Tok Noi, *Picheansoonthon 732* (holotype BKF; isotypes BK, SING).

18. ***Monolophus phuwoaensis*** (Picheans. & Koonterm) Veldk. & Mood, **comb. nov.** – *Caulokaempferia phuwoaensis* Picheans. & Koonterm, Taiwania 53: 248, t. 1, 2, 7 (2008). TYPE: Thailand, Nong, Khai, Amphoe Bung Khla, Pu Woa Wildlife Sanctuary, *Picheansoothon 723* (holotype BKF; isotypes BK, SING).

19. ***Monolophus saksuwaniae*** (K.Larsen) Veldk. & Mood, **comb. nov.** – *Caulokaempferia saksuwaniae* K.Larsen, Bot. Tidsskr. 68: 157, t. 1. (1973). TYPE: Thailand, Phangnga, Takuapa, Mt. Khao Pra Mi, *Larsen, Larsen, Nielsen & Santisuk 30832* (holotype AAU).

20. ***Monolophus satunensis*** (Picheans.) Veldk. & Mood, **comb. nov.** – *Caulokaempferia satunensis* Picheans., Folia Malaysiana 8: 56, t. 15 (2007). TYPE: Thailand, Satun, Thung Wa, Tan Pliu Waterfall, *Picheansoonthon 531* (holotype BKF; isotypes KEP, SING).

21. ***Monolophus saxicola*** (K.Larsen) Veldk. & Mood, **comb. nov.** – *Caulokaempferia saxicola* K.Larsen, Bot. Tidsskr. 60: 171, t. 3, 4 (1964). TYPE: Thailand, Prachinburi, Mt. Khao Khieo Hills, *Larsen s.n.* (holotype C).

22. ***Monolophus secundus*** (Wall.) Wall., Numer. List 6591 (1832) ("*secunda*"). – *Kaempferia secunda* Wall. in Roxb., Fl. Ind. 1: 19 (1820). – *Costus secundus* (Wall.) Spreng., Syst. Veg. 1: 13 (1824, "1825"). – *Caulokaempferia secunda* (Wall.) K.Larsen, Bot. Tidsskr. 60: 170 (1964).

TYPE: India, Silhet, *F.D. & W.G. (Da Silva and Gomez)* in *Wallich 6591* (holotype K; isotypes C, CAL, P, IDC microfiche 7394).

23. ***Monolophus sikkimensis*** (King ex Baker) Veldk. & Mood, **comb. nov.** – *Kaempferia sikkimensis* King ex Baker in Hook.f., Fl. Brit. India 6: 223 (1890). – *Caulokaempferia sikkimensis* (King ex Baker) K.Larsen, Bot. Tidsskr. 60: 169 (1964). TYPE: India, Sikkim, *Elwes s.n., Aug 1886* (lectotype K, designated here).

24. ***Monolophus sirirugsae*** (Ngamr.) Veldk. & Mood, **comb. nov. –** *Caulokaempferia sirirugsae* Ngamr., Nordic J. Bot. 26: 325, t. 1, 2 (2009). TYPE: Thailand, Phangnga, Khao Lumpee Waterfall, *Ngamriabsakul 51-01* (holotype BKF; isotypes PSU, Wailak Univ. Herb.).

25. ***Monolophus tamdaoensis*** (Picheans. & Inthar.) Veldk. & Mood, **comb. nov.** – *Caulokaempferia tamdaoensis* Picheans. & Inthar., J. Jap. Bot. 89: 134 (2014). TYPE: *Picheansoonthon & Phokham 180812-1* (holotype BK).

Appendix 2. Taxa excluded from *Monolophus* (name in bold is currently accepted name).

1. *Gastrochilus ochroleucus* Ridl., J. Straits Branch Roy. Asiat. Soc. 32: 109, 110. (1899) ("*ochroleuca*"). – *Kaempferia ochroleuca* (Ridl.) K.Schum. in Engler, Pflanzenr. IV, 46, Heft 20: 75. (1904). – ***Boesenbergia ochroleuca*** (Ridl.) Schltr. in Fedde, Repert. Spec. Nov. Regni Veg. 12: 316. (1913). TYPE: Thailand, between Kasum and Pungah, Ridley *Illustration 00754* (lectotype SING, designated by Turner 2000: 25–26, t. 2; isotype K?).
Note – Included in *Gastrochilus* Wall., non D. Don unranked § *Mesanthi* by Ridley (1899: 109) and in *Kaempferia* subg. *Monolophus* by Schumann (1904).

2. *Kaempferia* L. subg. *Pyrgophyllum* Gagnep., Bull. Soc. Bot. France 48: lxxviii (1902, "1901"). – *Camptandra* Ridl. sect. *Pyrgophyllum* (Gagnep.) Gagnep. ex K.Schum. in Engler, Pflanzenr. IV, 46, Heft 20: 63 (1904). – *Caulokaempferia* K.Larsen sect. *Pyrgophyllum* (Gagnep.) R.M.Sm., Notes Roy. Bot. Gard. Edinburgh 31: 291 (1972). – ***Pyrgophyllum*** (Gagnep.) T.L.Wu & Z.Y.Chen, Acta Phytotax. Sin. 27: 126 (1989). TYPE: *Kaempferia yunnanensis* Gagnep.
Note – *Pyrgophyllum* in our analysis (Fig. 1) is distinct from *Monolophus* (see below #10).

3. *Kaempferia decus-sylvae* Hallier f., Ann. Jard. Bot. Buitenzorg 13: 321, t. 27, f. 4. (1896). – ***Haplochorema decus-sylvae*** (Hallier f.) Valeton, Bull. Jard. Bot. Buitenzorg ser. II, 27: 116. (1918). TYPE: Indonesia, Kalimantan, Liang Gagang Mts, *Hallier 2636* (lectotype L [122322 spirit], designated here; isotype BO).
Note – Attributed to *Kaempferia* sect. *Monolophus* by Hallier.

4. ***Kaempferia elegans*** Wall., Pl. Asiat. Rar. 24, t. 27 (1829). – *Monolophus elegans* (Wall.) Wall., Numer. List 6593 (1832); Horan., Prodr. Monogr. Scitam.: 22 (1862). TYPE: Wallich (1829) cited "Pegu, Martaban, Rangoon, Amherst, Moalmyne". Only the Rangoon locality is mentioned in the Wallich Herbarium, K-W. We here select *6593-A, bottom specimen* (lectotype K-W [IDC microfiche 7394], first step designation by Picheansoonthon & Koonterm (2008b: 77, "Tenasserim"), second step designated here: Birma, Rangoon.
Note – Included in *Kaempferia* subg. *Monolophus* by Baker (1892).

5. *Kaempferia gracillima* K.Schum. in Engler, Pflanzenr. IV, 46, Heft 20: 74 (1904). – *Camptandra gracillima* (K.Schum.) Valeton, Bull. Jard. Bot. Buitenzorg II, 27: 115. (1918). TYPE: Sarawak, Selebut, *Haviland 448* (holotype B, lost; isotype K). = ***Camptandra parvula*** (King ex Baker) Ridl. var. ***angustifolia*** Ridl., fide Newman et al. (2004: 61).
Note – Included in *Kaempferia* subg. *Monolophus* by Schumann (1904: 74).

6. *Kaempferia macrochlamys* Baker in Hook.f., Fl. Brit. India 6: 223. 1892. – ***Stahlianthus macrochlamys*** (Baker) Craib, Bull. Misc. Inform. Kew. 1912: 401 (1912). TYPE: Burma, Tenasserim, *Parish s.n.* (holotype K).
Note –Included in *Kaempferia* subg. *Monolophus* by Baker (1892).

7. *Kaempferia parvula* King ex Baker in Hook.f., Fl. Brit. India 6: 223 (1892). – ***Camptandra parvula*** (King ex Baker) Ridl., J. Straits Branch Roy. Asiat. Soc. 32: 104. (1899). TYPE: Malay Peninsula, Goping, *King's collector* (holotype K [000255350]; isotype CAL, K).
Note – Included in *Kaempferia* subg. *Monolophus* by Baker.

8. ***Kaempferia philippinensis*** Merr., Philipp. J. Sci., sect. C, Bot. 10: 296 (1915). TYPE: Philippines, Luzon, Laguna, San Antonio, Dahican River, *Ramos BS 14952* (holotype PNH, lost).
Note – Included in *Kaempferia* subg. *Monolophus* by Loesener (1930: 566) and Merrill (1934).

9. Kaempferia siphonantha King ex Baker in Hook.f., Fl. Brit. India 6: 222 (1892). – ***Boesenbergia siphonantha*** (King ex Baker) M.Sabu et al., Rheedea 14: 55, t.1, 2. 2004. TYPE: Andaman Isl., *King's collector 372* (probably *Kunstler*) (holotype K [000640517]; isotype CAL).
Note – Included in *Kaempferia* subg. *Monolophus* by Baker (1892).

10. *Kaempferia yunnanensis* Gagnep., Bull. Soc. Bot. France 48: lxxvii (1901). – *Camptandra yunnanensis* (Gagnep.) K.Schum. in Engler, Pflanzenr. IV, 46, Heft 20: 64. (1904). – *Caulokaempferia yunnanensis* (Gagnep.) R.M.Sm., Notes Bot. Gard. Edinburgh 31: 292, t. 2. (1972). – *Monolophus yunnanensis* (Gagnep.) T.L.Wu & S.J.Chen in Anon., Iconogr. Cormophyt. Sin. 5: 586, t. 8001 (1976), nom. inval., sine basion.; T.L.Wu & S.J.Chen ("Senjen") Acta Phytotax. Sin. 16(3): 29 (1978). – ***Pyrgophyllum yunnanensis*** (Gagnep.) T.L.Wu & Z.Y.Chen, Acta Phytotax. Sin. 27: 127 (1989). TYPE: China, Yunnan, N of Tali, Tsong-so gorges (Ten tchouan), *Delavay 2721* (holotype P; isotype E).
Kaempferia fongyuensis Gagnep., Bull. Soc. Bot. France 48: lxxviii (1901). – *Camptandra fongyuensis* (Gagnep.) K.Schum. in Engler, Pflanzenr. IV, 46, Heft 20: 64. (1904). TYPE: China, Yunnan, Fung-Yu, near Er'Haï lake, *d'Orleans s.n., 19 Jun* (holotype P) (synonymy fide Wu & Chen, 1978: 29).

11. *Monolophus philippianus* A.Dietr., Allg. Gartenz. 17: 266 (1849). – *Kaempferia philippiana* (A.Dietr.) K.Schum. in Engler, Pflanzenr. IV, 46, Heft 20: 85 (1904). – ***Stahlianthus philippianus*** (A.Dietr.) Loes. in Engler, Nat. Pflanzenfam., ed. 2, 15a: 564 (1930). TYPE: From India, sent to Reinecke of the Decker Garten, Berlin, flowered in 1849, *Philippi Aº 1846* (holotype B, lost).

12. *Monolophus scaposus* (Nimmo) Dalzell in Hook., J. Bot. Kew Gard. Misc. 2: 143 (1850). – *Hedychium scaposum* Nimmo in Graham, Cat. Pl. Bombay: 205 (1839). – *Kaempferia scaposa* (Nimmo) Benth. in Benth. & Hook.f., Gen. Pl. 3: 642 (1883). – ***Curcuma scaposa*** (Nimmo)

Škorničk. & M.Sabu, Ann. Bot. (Oxford) 100: 524 (2007). TYPE: India, southern Concan, *King s.n.* (neotype BM, designated by Leong-Škorničková et al. (2007); isoneotype K).
Note – Included in *Kaempferia* L. sect. *Stachyanthesis* Benth. (1883). According to Leong-Škorničková et al. (2007) *Hedychium scaposum* Nimmo is the basionym of *Monolophus scaposus* even though the name was not mentioned by Dalzell (1850). Later, Dalzell & Gibson (1861) described *Hedychium scaposum* Nimmo with *M. scaposus* Dalz. in synonymy. Under Art 41.4 of the *ICN*, even though there is no reference to a basionym, Dalzell's intention is obvious and Nimmo is to be accepted as the author of the basionym. As no Graham nor Nimmo material apparently exists Leong-Škorničková et al. (2007) designated a neotype.

Appendix 3. New *Boesenbergia* combinations.

Boesenbergia Kuntze, Revis. Gen. Pl. 2 (1891) 685. – *Gastrochilus* Wall., Pl. Asiat. Rar. 1 (1829) 22. TYPE: *Boesenbergia pulcherrima* (Wall.) Kuntze, lectotype designated by Holttum (1950: 107).
Jirawongsea Picheans., Folia Malaysiana 9:2 (2008). TYPE: *Jirawongsea laotica* (Picheans. & Mokkamul) Picheans.

1. ***Boesenbergia alba*** (K.Larsen & R.M.Sm.) Mood & L.M.Prince, **comb. nov.** – *Caulokaempferia alba* K.Larsen & R.M.Sm., Notes Roy. Bot. Gard. Edinburgh 31: 288, t. 1 (1972). – *Jirawongsea alba* (K.Larsen & R.M.Sm.) Picheans., Folia Malaysiana 9: 3, t. 1–4. (2008). TYPE: Thailand, Phitsanulok, summit Phu Mieng, *Smitinand & Warncke 949* (holotype AAU; isotype BKF).

2. ***Boesenbergia burttii*** (K.Larsen & Jenjitt.) Mood & L.M.Prince, **comb. nov.** – *Caulokaempferia burttii* K.Larsen & Jenjitt., Edinburgh J. Bot. 60: 509, t. 1. (2004). – *Jirawongsea burttii* (K.Larsen & Jenjitt.) Picheans, Folia Malaysiana 9: 3, t. 5–8 (2008). TYPE: Laos, Champassak, Paksong (Bolaven Plateau), *Jenjittikul 8263* (holotype AAU; isotypes BKF, E, PBM).

3. ***Boesenbergia laotica*** (Picheans. & Mokkamul) Mood & L.M.Prince, **comb. nov.** – *Caulokaempferia laotica* Picheans. & Mokkamul, Nat. Hist. Bull. Siam Soc. 54: 75, t. 1–5. (2006). – *Jirawongsea laotica* (Picheans. & Mokkamul) Picheans., Folia Malaysiana 9: 4, t. 7, 8 (2008). TYPE: Laos, Champasak, Phu Luang, Bolaven Plateau, *Picheansoonthon 581* (holotype BKF; isotype SING),

4. ***Boesenbergia thailandica*** (K.Larsen) Mood & L.M.Prince, **comb. nov.** – *Caulokaempferia thailandica* K.Larsen, Bot. Tidsskr. 68: 157, t. 2. (1973). TYPE: Thailand, Loei, Phu Kradung, *Smitinand 336* (holotype BKF).

5. ***Boesenbergia violacea*** (K.Larsen & Triboun) Mood & L.M.Prince, **comb. nov.** – *Caulokaempferia violacea* K.Larsen & Triboun in K.Larsen, Nordic J. Bot. 22: 414, t. 3, 4. (2003). TYPE: Thailand, Loei, Phu Rhua, *Triboun 399* (holotype BK; isotypes AAU, BKF).

Appendix 4: GenBank accession numbers for Zingiberaceae used in this study. Format: identification, plant sample number [for newly sequenced samples] (collector and voucher number, herbarium), ITS GenBank number/*trnK* GenBank number.

Boesenbergia alba (K.Larsen & R.M.Sm.) Mood & L.M.Prince: *M3253* (*Mood 3253*, BISH) KF982792/KF982801.
Boesenbergia alba (K.Larsen & R.M.Sm.) Mood & L.M.Prince: *M12C30* (*Funakoshi s.n.*, MBK) KF982793/KF982802.
Boesenbergia burttii (K.Larsen & Jenjitt.) Mood & L.M.Prince: *M12C32 (Funakoshi s.n.*, MBK) KF982794/KF982803.
Boesenbergia curtisii (Baker) Schltr.: *M1739* (*Mood 1739*, BISH) KF982795/KF982804
Boesenbergia hamiltonii Mood, S. Dey & L.M.Prince: *M3017* (*Mood 3017*, BISH) JX992754/ JX992815.
Boesenbergia plicata* var. *lurida Holttum: *M3120* (*Mood & Vatcharakorn 3120*, BK) JX992808/JX992839.
Boesenbergia pulcherrima (Wall.) Kuntze: *M08P276* (*Mood 08P276*, BISH) X992809/ JX992748.
Boesenbergia rotunda (L.) Mansf.: (*Kress 00-6737*, US) AF478726/AF478726.
Boesenbergia thailandica (K.Larsen) Mood & L.M.Prince: (*Ngamriabsakul 61*, BKF) AY424748/--.
Boesenbergia violacea (K.Larsen & Triboun) Mood & L.M.Prince: *M12C31* (*Funakoshi s.n.*, MBK) KF982796/KF982805.
Camptandra parvula (King ex Baker) Ridley: (*Kress 99-6328*, US) AF478730/AF478830.
Cornukaempferia aurantiflora Mood & K.Larsen: (*Kress 01-6983*, US) AF478736/AF478835.
Distichochlamys rubrostriata W.J.Kress & Rhese: (*Kress 01-6848*, US) AF478745/AF478844.
Globba curtisii Holttum: (*Kress 99-6347*, US) AF478754/AF478853.
Haniffia albiflora K.Larsen & Mood: *(Kress 99-6370*, US) AF478756/AF478855.
Hedychium bordelonianum W.J.Kress & K.J.Williams: (*Kress 99-6462*, US) AF478757/ AF478856.
Hemiorchis rhodorrhachis K.Schum.**:** (*Newman 861*, E) AF478763/ AF478863.
Hitchenia glauca Wall.: (*Kress 00-6743* US) AF478765/AF478864.
Hornstedtia hainanensis T.L.Wu & S.J.Chen: (*Kress 97-5769*, US) AF478766/AF478865.
Kaempferia rotunda L.: (*Kress 99-6304*, US) AF478767/AF478868.
Monolophus coenobialis Hance: (unknown) HM236121/--.
Monolophus limianus (Mokkamul & Picheans.) Veldk. & Mood.: *M3246* (*Mood 3246*, BISH) KF982797/KF982806.
Monolophus linearis (Wall.) Wall.: *M12C193 (Dey NU198*, CAL) KF982798/KF982807.
Monolophus saxicola (K.Larsen) Veldk. & Mood: *M12C29* (*Funakoshi s.n.*, MBK) KF982799/ KF982808.
Monolophus sikkimensis (King ex Baker) Veldk. & Mood: *New2458* (*Newman 2458*, spirit, E) KF982800/KF982809.
Pommereschea lackneri Witt.: (*Kress 00-6739*, US) AF478776/AF478877.
Pyrgophyllum yunnanense (Gagnep.) T.L.Wu & Z.Y.Chen: (*Kress 00-6596*, US) AF478777/ AF478878.
Rhynchanthus beesianus W.W.Sm.: (*Kress 97-5827*, US) AF478784/AF478885.
Roscoea purpurea Sm.: (*Kress 01-6953*, US) AF478787/AF478888.
Siliquamomum tonkinense Baill.: (*Kress 00-6802*, US) AF478791/AF478892.
Siphonochilus kirkii **(**Hook.f.) B.L.Burtt: (*Kress 94-3692*, US) AF478794/AF478895.
Tamijia flagellaris S.Sakai & Nagam.: (*Kazuyuki S55*, KYOTO) AF478797/AF478898.
Zingiber gramineum Noronha ex Blume: (*Kress 96-5739*, US) AF478800/AF478902.