THAI FOREST BULL., BOT. 46(1): 10–24. 2018.
DOI https://doi.org/10.20531/tfb.2018.46.1.03

Taxonomy of *Boesenbergia parvula* (Zingiberaceae) with new synonymy

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ABSTRACT

The taxonomy and botanical history of *Boesenbergia gelatinosa* K. Larsen, *B. jahaiana* Meekiong & C.K.Lim, *B. parvula* (Wall.) Kuntze, and *B. phyllostachya* (Gagnep.) K.Larsen are reviewed as a group with similar characteristics. Based on morphological comparisons, ecological data, and molecular phylogenetic analyses using plastid and nuclear DNA sequence data, these species are determined to be conspecific with *B. parvula* and are here made synonyms. A new variety, *B. parvula* var. *major* Mood & Veldkamp is described.

KEYWORDS: Asexual propagule, axillary branching, Lao P.D.R., molecular phylogeny, Malaysia, Myanmar, Thailand, Vietnam.

Published online: 30 March 2018

INTRODUCTION

Boesenbergia Kuntze (Zingiberaceae) is a genus of relatively small, herbaceous plants found mostly in the forest understorey, although a few species can be found in more diverse habitats such as open, sandstone plateaux [*B. alba* (K.Larsen & R.M.Smith) Mood & L.M.Prince] and exposed limestone outcrops near the ocean [*B. ochroleuca* (Ridl.) Schltr.]. Currently, ca 70 species are recognized with a distribution from the Western Ghats of India eastward into the Philippine Is., and from Nepal, south to Wallace's Line.

In August 2011, during a collection trip for the Flora of Thailand Project, four *Boesenbergia* collections were made between Kanchanaburi and Ranong Provinces—[*Mood & Vatcharakorn 3070* (**BKF**), *3076* (**BKF**), *3100* (**BKF**), & *3112* (**BKF**)]. The following year, similar plants were found in Yala Province, ca 20 km north of the Malaysian border [*Mood & Vatcharakorn 3309* (**BKF**)] and in Chanthaburi Province [*Mood & Vatcharakorn 3282* (**BKF**)] in SE Thailand. After a specimen and literature review, these six taxa were found to be very similar to *B. gelatinosa* K.Larsen, *B. parvula* (Wall.) Kuntze, and *B. phyllostachya* (Gagnep.) K.Larsen. Over the next two years, more populations of similar species were discovered from which specimens and living plants were collected for study. These sites included the type localities of *B. gelatinosa* and *B. parvula*. Separately, the second author obtained material of *B. phyllostachya* near the type locality in Vietnam in 2009.

While comparing these collections, it was recognized that all of the specimens had two rare characters in common—a non-rhizomatous, perennating organ and axillary branching. Bulbils were also observed on all but *B. phyllostachya*. The only other *Boesenbergia* species which are known by the authors to have at least two of these three characters are *B. ochroleuca* (Ridl.) Schltr. and *B. siamensis* (Gagnep.) Sirirugsa. After a review of the accumulated data, it appeared that *Boesenbergia gelatinosa*, *B. jahaiana*, *B. parvula*, and *B. phyllostachya* were most likely conspecific.

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HISTORY

Boesenbergia parvula (Wall.) Kuntze was first collected in 1827 by William Gomez, a collector for Nathaniel Wallich. This very small ginger plant was found in the mountains east of Tavoy without a precise locality in southern Myanmar (Tenasserim). Although it was discovered prior to Wallich's publication on *Gastrochilus* Wall. (1829), it was not included there, but later documented in 1832 as *Gastrochilus parvula* Wall. [*Wallich 6590* (**K-W**)]. This specimen was eventually described by Baker in 1890 where he called it a "dwarf annual". A year later, Kuntze (1891) determined that *Gastrochilus* Wall. was a homonym of the Orchidaceae genus *Gastrochilus* D.Don (1825) and changed the ginger genus to *Boesenbergia* Kuntze. It appears that the next collection in Burma of *B. parvula* was not made until August 1908 and then in a distant region, ca 950 km north of Tavoy at Goke Hteik Gorge, Shan State [*Lace 4153* (**E**)]. In 1961, J. Keenan (RBGE), quite by chance while awaiting clearance to collect in Shan State, Myanmar, was allowed into the Tenasserim Division. Although not specifically studying gingers, he noted that in the Baungdaw area, *B. parvula* was "common, abundant, plentiful and frequently seen" where he subsequently collected five specimens (E). The first author attempted to go to Baungdaw in 2014 but, due to floods, only got to within ca 10 km. Even so, *B. parvula* was observed in abundance along many streams in the area.

As noted by Craib (1913), the first record in Thailand of *Boesenbergia parvula* was from Doi Sutep, Chiang Mai Province [*Kerr 737* (**K**)]. In the following years, over 80 specimens annotated as this species were collected in 20 Thai provinces from Chiang Rai [*Norsaengsri & Tathana 9745* (**QBG**)] to Yala [*Mood & Vatcharakorn 3309* (**BKF**)]. Recently, a collection was made in the Louangphabang area, Lao P.D.R. [*Leong-Skornickova 1694* (**SING**)] and another observation made nearby (wild in situ) at Pha Tad Ke Botanical Garden (Chalermglin, TISTR). Further new collections have been made in southern Myanmar (Mood *et al.* 2016 b).

Boesenbergia phyllostachya (Gagnep.) K.Larsen was described in 1906 from several 19th century specimens from Cochinchina (Vietnam) [*Pierre s.n.* (**P**)]. At the time Gagnepain, like others, e.g., Ridley, Schumann, and Valeton, did not follow Kuntze's generic nomenclature. Even though other Gastrochilus species were transferred during the intervening years, this epithet was overlooked until 1997. Even then, this change was technically invalid as the basionym was cited without "a full and direct reference given to its author and place of valid publication", and without page or plate reference and date (ICN Art. 41.5, see also Art. 41.6 and 41.8). This has since been corrected (Veldkamp, 2014). Larsen also designated a lectotype, "*Pierre s.n.* Vietnam: Ri-hao, Sept. 1865 (**P**)". This location and date are found in the protologue, but are not annotated on the lectotype nor two other similar Pierre specimens. The only other collection known from major herbaria which appears to be this species is *Trần 160* (**E**, **SING**, **VMN**) from Dak Nong Province, Vietnam.

Boesenbergia gelatinosa was described in 1997 based on a single collection from Kaeng Kra Chan NP, Thailand [*Larsen et al. 45428* (**AAU, K**)]. In the protologue, it was diagnosed against *B. longipes* (King & Prain ex Ridl.) Schltr. Recently, it was determined that this epithet (*B. longipes*), as used in Thailand, represented a different taxon than the type from Perak, Malaysia. Consequently, the Thai species against which Larsen diagnosed *B. gelatinosa* is now *B. purpureorubra* Mood & L.M.Prince (Mood *et al.*, 2014a) which has no close similarity or affinity to *B. gelatinosa*.

Boesenbergia jahaiana was described in 2014 from specimens from a single population found in Belum Forest Reserve, Perak, Malaysia. Similar plants have also been found in Kelantan, Malaysia (pers. com. FRIM).

MATERIALS AND METHODS

Field work was conducted from 2010 through 2015. Over 20 sites were visited to include the type localities of *Boesenbergia gelatinosa* and *B. parvula*, and an area very close to the type locality of *B. jahaiana*. The ecology at each site was documented to include photography with herbarium specimens, living plants, and silica dried leaf samples collected. Follow-on observations of the living plants grown was documented over several growing seasons with measurements and photographs. During the study, over 100 herbarium specimens were examined that were either previously identified as one of the four species,

misidentified as another species, or undetermined, but with similarity to *B. parvula*. In the case of *B. phyllostachya*, preliminary research was accomplished by the second author in 2009 when the species was collected in Dak Nong Province, Vietnam near the type locality. This study provided a fertile specimen with a complete description, tissue sample, and photographs.

In 2014, a living plant of *Boesenbergia* cf. *parvula* was obtained from the Lao P.D.R. with a tissue sample. The final study of herbarium specimens and molecular analyses were completed in 2016.

Molecular Phylogeny

Leaf tissue samples were obtained as described above. The authors have a large, on-going research project in *Boesenbergia* that provided additional scaffold sequences. Those sequences, along with representatives of 31 other genera, were combined with data downloaded from GenBank. A list of relevant samples (with associated GenBank accession numbers) is provided in Appendix 1.

As with prior publications by the authors, DNA extraction follows Kress *et al.* (2002) while amplification and analytical methods follow Mood *et al.* (2013). The nuclear ribosomal ITS (nrITS) region was amplified using the plant specific18S-F (CGATTGAATGGTCCGGTGAAG) and 26S-R (AGGACGCTTCTACAGACTACAA) primers (both published in Prince, 2010). The plastid *trnK* region was amplified in two parts, the first using either 1F (CTCAACGGTAGAGTACTCG; Manos & Steele, 1997) and mIR (CGTTTCACAAGTACTGAACTA) or 1F and 1235R (TATACTAATACCCCACYCC). The second half was amplified using mIF (GTTCAGTACTTGTGAAACGTT; Kress *et al.*, 2002) and 2R (AACTAGTCGGATGGAGTAG; Steele & Vilgalys, 1994). Data were visualized on an ABI Genetic Analyzer and sequences were verified and edited in Sequencher v4.9 (Gene Codes Corporation, Ann Arbor, Michigan, USA). Consensus sequences were aligned in Se-al (Rambaut, 1996).

Data analyses were conducted under maximum parsimony criteria in PAUP* (version 4.0b10; Swofford, 2002). Exploratory heuristic searches of the family-wide data matrices were limited to 10,000 random addition replicates, saving 10 trees per replicate. *Siphonochilus* was selected as the outgroup taxon for these exploratory searches since it has previously been identified as the first diverging lineage in the family (Kress *et al.* 2002). Similarly, bootstrap analyses of the large data matrix were limited to 100,000 fast swap replicates. Alignment of sequences across the family were challenging for the ITS region and the effect of alternative alignments or the exclusion of ambiguously aligned regions on resulting topologies were qualitatively compared. More extensive heuristic search methods were conducted (1000 random addition replicates, saving all shortest trees) with a subset of sequences to allow less ambiguity in the DNA sequence alignment in the target clade. *Boesenbergia rotunda* was selected as the outgroup taxon for these searches. Branch support was estimated using heuristic search parameters in a parsimony bootstrap (BS) in PAUP*.

RESULTS AND DISCUSSION

Exploratory family-wide analyses of ITS sequences identified a strongly supported *Boesenbergia parvula sensu lato* clade (100% fast BS; results not shown) containing 19 ingroup sequences, which was confirmed in analyses of the *trnK* data partition (78% fast BS; results not shown). Analyses of sequences in the target clade (plus a few place holder samples) also result in a strongly supported (99% BS for each data partition, 100% for the combined data matrix), monophyletic *B. parvula* clade. Resolution within the clade was limited and bootstrap support was generally weak (BS <70%) whether the data partitions were analyzed separately (results not shown) or in combination (Fig. 1). This is likely due to the small number of potentially parsimony informative characters (PIC) in the dataset. The *trnK* matrix provided 13 PIC (five for the ingroup) and the ITS 45 (only 13 for the ingroup). Variable characters were inferred to be homoplasious when the characters were traced onto the most parsimonious trees using MacClade (Maddison & Maddison, 2000).

TAXONOMY

Boesenbergia parvula (Wall. ex Baker) Kuntze, Revis. Gen. Pl. 2: 685. 1891.— *Gastrochilus parvulus* Wall. ex Baker in Hook.f., Fl. Brit. India 6: 218 ("*parvula*") 1890. Type: Burma, Tavoy, 1827, *Gomez*, W. in Wallich, N. 6590 (**K-W!**).— *Boesenbergia gelatinosa* K.Larsen, Nordic J. Bot. 17: 361, t. 1.

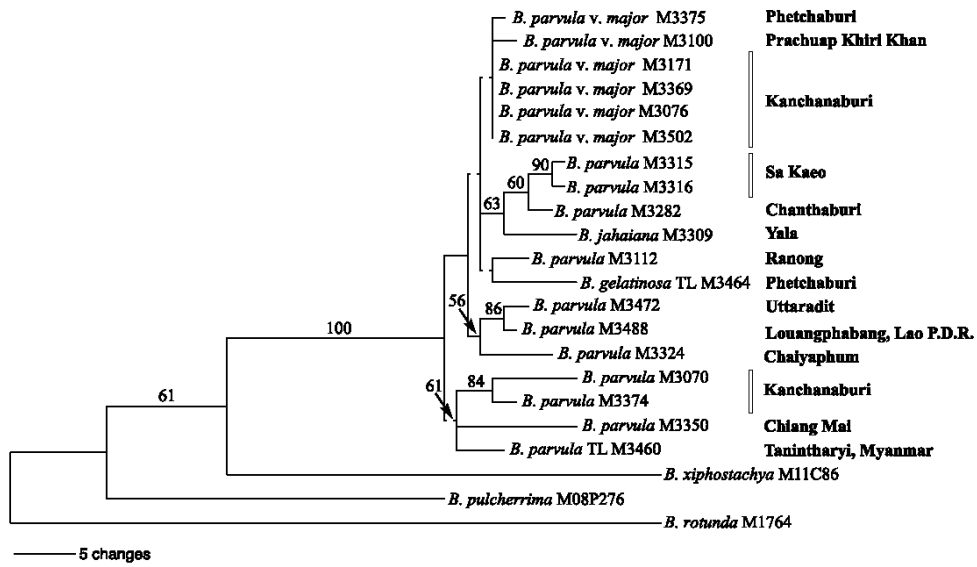

Figure 1. Phylogram of one of 46 shortest trees for *Boesenbergia parvula* based on maximum parsimony analysis of *trnK* and ITS sequence data. Numbers above the branches are maximum parsimony bootstrap values. (TL = type locality). The four branches that collapse in the maximum parsimony strict consensus tree are indicated with a dashed line. Regional locality of samples on far right.

1997. Type: Thailand, Phetchaburi Province, Kaeng Kra Chan NP, 1995, *Larsen et al. 45428* (holo **AAU!**, iso **K!**).— *B. jahaiana* Meekiong & C.K.Lim, Folia Malaysiana 15: 41–50. 2014. Type: Malaysia, Perak, Belum Forest Reserve, Aug. 2007, *Meekiong MK1388* (holo **UKMB**).— *B. phyllostachya* (Gagnep.) K.Larsen.— *Gastrochilus phyllostachyus* Gagnep., Bull. Soc. Bot. France 53: 146. ("*phyllostachyum*"). 1906.— *Boesenbergia phyllostachya* (Gagnep.) K.Larsen (Nordic J. Bot. 17: 363. 1997, *nom. inval.*, sine basionym ref.) ex Veldkamp, Philipp. J. Sci. 142: 220. 2014. Type: Vietnam, Ri-hao, *Pierre s.n.*, Sept. 1865, (lectotype **P!**, *P032701*; isolectotypes **P!**, *P00686541*, *P00686542* designated here). Figs. 2–9.

Deciduous, perennial herb to (10)–30–(50) cm, upright to prostrate. *Perennating organ*, a bud-crowned tuberous root, cylindrical, 1–13 cm long, to ca 2 cm diam., often in multiples attached together at the proximal end, internally and externally white, covered in short roots; roots few, fleshy, to ca 3 mm, fibrous roots few, short. *Stems* succulent, internodes short, branched from the lower leaf axils; leafless sheaths corrugate, red or green. *Leaves* alternating along the stem, ca 5–7, mostly congested near the terminus; leaf sheaths 1–3, ca 2 cm long, corrugate, red or green; ligule bilobed, to ca 5 mm, lobes triangular, green; petiole subsessile to ca 2 cm, ribbed; lamina oval, to ca 10 × 5 cm, base attenuate, apex acuminate, adaxially green, with or without a darker centre and silver margins, glabrous, abaxially green or reddish, mostly glabrous. *Inflorescence* terminal on the main stem and axillary stems, tightly clasped between the leaf sheaths, partially exserted, mucilaginous; peduncle to 1 cm, white; spike fusiform, to ca 4 cm long; bracts distichous, lanceolate, to ca 3 cm long, apex acuminate, green or red, covered portions white, glabrous, finely striate; bracteole lanceolate, to ca 2.5 cm long, green or white, glabrous. *Flowers* 3–7, ca 3 cm long, orientated 90° to the bract, deflexed downward; calyx ca 3 mm long, white, translucent, apex irregular; floral tube ca 1.5–3.5 cm long, white, glabrous; dorsal and lateral corolla lobes ovate, ca 10 × 5 mm, apex cucullate, white, glabrous; androecial cup ca 5 mm long, orientated ca 90° to the floral tube, throat with hairs; labellum deeply saccate, nearly orbicular, ca 2.5 × 2 cm, white with various red patterns, glabrous, apex entire, margins deflexed; lateral staminodes obovate,

7 × 5 mm, white, glabrous. *Stamen* ca 9 mm long, white, glandular hairy throughout; filament ca 2 mm long; anther 6 × 3 mm, white, thecae 5 × 1.5 mm, dehiscent along their full length, anther crest absent. *Ovary* cylindrical, ca 3 × 2 mm, white, glabrous; style filiform, ca 4 cm long, white; stigma orbicular, white, ostiole circular, ciliate; epigynous glands two, ca 2 mm long, light green. *Fruit* cylindrical, ca 12 mm long, tan; seed elongate ca 6 × 2 mm, brown, hirsutulous, aril medusa-form, ca 3 mm long, white, translucent, funiculus ca 2 mm diam., white. *Bulbils* cylindrical, ca 1–1.5 × 0.7 cm, green, sericeous occurring at the stem nodes.

Distribution.— Lao P.D.R., Myanmar, Peninsular Malaysia, Thailand, Vietnam.

Ecology.— The populations studied were found in both evergreen and deciduous forests. More often than not, bamboo was a large part of the immediate overstorey. Each site was generally similar in having well-drained soil, high in organic matter with a heavy cover of leaf litter, medium to heavy shade, and a tendency to be situated on a slope near a watercourse. In a few situations, the species was found in areas growing amongst scattered limestone boulders on dark, humus-rich soil. In all cases, the sites were verdant with plenty of soil moisture and high humidity. All populations had a very high plant density per m^2, encompassing multiple stages of growth from very small seedlings/rooted bulbils to mature, multi-year plants. At many sites, the populations tended to be large, covering 10–20 m^2. The associated understorey plants were typical of SE Asian forests to include Commelinaceae, Marantaceae, and other Zingiberaceae. Elevation ranged from 200–1000 m asl.

Phenology.— Over five years of field observations, no large insects (bees, beetles, wasps) or birds were ever observed pollinating, although plenty of smaller flying insects and ants could be found most times in and about the flowers. Flowering begins in mid-June and continues into October.

Etymology.— Named for the small plant size as represented by the type.

Additional specimens examined: LAO P.D.R. Louangphabang: *Leong-Skornickova 1694* (**SING**); Pha Tad Ke B.G., 15 July 2014, *Mood & Chalermglin 3488* (**BKF**). MALAYSIA. Perak: Belum Forest Reserve, 25 Aug. 2007, *Meekiong MK1388* (holo **UKMB**). MYANMAR. Shan State: Goke Hteik Gorge, 2 Aug. 1908, *Lace 4153* (**E**); Tanintharyi: area within 20 km from Baungdaw, 200–640 m asl, Aug.–Sept. 1961, *Keenan 738, 829, 971, 1008, 1399* (**E**); Northeast of Baungdaw, ca 15 km, 14° 11.714′N 98° 36.955′E, 190 m asl, 11 July 2014, *Mood & Chalermglin 3460* (**BKF**). THAILAND. NORTHERN: Mae Hong Son [Tham Pla-Namtok Pha Suea NP, Mueang, Pha Suea Waterfalls, 446 m asl, 21 Aug. 2013, *Norsaengsri 10538* (**QBG**)]; Nan [Na Noi Dist., Sisaket Subdist., Sri Nan NP, 850 m asl, 11 Aug. 2004, *Maxwell 04-345* (**CMUB**); Doi Phu Kha NP, Pua, 950 m asl, 24 Aug. 2001, *Srisanga & Maknoi 2099* (**QBG**); Tham Pha Kong, Doi Phu Kha NP, Pua, 870 m asl, 26 June 2002, *Srisanga 2530* (**QBG**); Pha Luak, Ban Pha Luck, Yod Subdist., Song Khwae, 16 July 2012, *La-ongsri et al. 2418* (**QBG**)]; Chiang Mai [Doi Anka (Sutep), 1440 m asl, 8 Aug. 1927, *Garrett 414* (**C, P**); Doi Sa Kap, 3 Aug. 1953, *Kerr s.n.* (**P01764011**); Doi Sutep, 900–1100 m asl, 20 Sept. 1967, *Shimizu & Hutoh 10554* (**BKF**); Doi Sutep, 1090 m asl, 12 Aug. 1968, *Phengnaren s.n.* (**BKF**); Doi Sutep, 1500 m asl, 4 Aug. 1988, *Maxwell 88-960* (**BKF**); Doi Pui, summit, 1580 m asl, 29 Sept. 2005, *Tillich 5055* (**BKF**); Inthanon NP, 850 m asl, 22 July 1988, *Phengklai et al. 6758* (**BKF**); Inthanon NP, 950 m asl, 23 July 1988, *Phengklai et al. 6839* (**BKF**); Doi Sutep, 8 July 1948, *Soradet 28* (**BKF**); Doi Sutep, 1500 m asl, 17 Sept. 2008, *Middleton et al. 4458* (BKF); To Mae Pan Waterfall, 1000–1300 m asl, 2 Aug. 1988, *Tamura T-60371* (**BKF**); Doi Sutep, 8 Aug. 1988, *Tamura et al. T-60675* (**BKF**); Doi Sutep, 1480 m asl, 8 Aug. 1988, *Tamura et al. T-60709* (**BKF**); Doi Sutep, 625 m asl, 22 June 1988, *Maxwell 88-791* (**BKF, CMUB**); Doi Sutep, 1125 m asl, 3 Sept. 1992, *Maxwell 71* (**BKF**, **CMUB**); Hang Dong Dist., Nahm Soom village, 975 m asl, 19 Aug. 2004, *Maxwell 04-380* (**CMUB**); Doi Chieng Dao, 700 m asl, 15 Aug. 1963, *Smitinand et al. 1016* (**BKF**); Doi Inthanon, along Mae Aep River, 580–620 m asl, 20 July 1988, *Tsugaru T-61647* (**QBG**); Doi Sutep-Pui NP, Tham Ruesi, 1150 m asl, 26 July 2013, *Newman et al. 2557* (**QBG**); Doi Sutep-Pui NP, 1062 m asl, 15 June 2012, *Norsaengsri et al. 9419* (**QBG**); Doi Sutep, 1000 m asl, 17 June 1958, *Larsen 3639* (**C**); Doi Sutep, 8 July 1958, *Larsen 3937* (**C**); Doi Sutep, 1100 m asl, 2 Sept. 1958, *Larsen 4666* (**C**); Doi Sutep, 800 m asl, 3 July 1958, *Larsen 3869* (**C**); Doi Inthanon, 15 Sept. 1995, *Larsen 46443*

(**BKF**); Doi Sutep, Monthathan Waterfall, 550 m asl, 17 Aug. 2004, *Nielsen et al. 1712* (**BKF**); Fang Dist., 10 km west of Fang, 600 m asl, 23 July 1968, *Larsen 2601* (**BKF**); Huei Cork Maa, 1250 m asl, 22 Sept. 1998, *Pongamornkul 315* (**QBG**); Doi Lahn, Mae Lie Village, 1075 m asl, 17 June 2005, *Maxwell 05-403* (**BKF, CMUB**); Mae-On, Huai Kaeo Trail, 1100 m asl, 7 Sept. 2011, *Pooma et al. 7787* (**BKF**); Doi Nang Non, Mae Fa Luang, ca 1000 m asl, 27 Aug. 2000, *Watthana 852* (**QBG**); Den Ya Khat, Doi Chiang Dao, Chiang Dao, 1500 m asl, 4 Aug. 2007, *Watthana 2423* (**QBG**); Huai Mae, QBG, Mae Rim, 20 July 1996, BAO. *Staff 6933* (**QBG**); Pa Pae, 19° 07.500′N 98° 44.591′E, 790 m, July 2013, *Mood & Vatcharakorn 3350* (**BKF**); Doi Sutep, 18° 48.068′N 98° 56.027′E, Aug. 2014, *Mood 3406* (**BKF**)]; Chiang Rai [Pong Dist., Phu Lung Ka, 30 Dec. 1954, *Royal Forest Dept. 9569* (**BKF**); Khun Nan Nang Norn FP, Mae Sai, 450 m asl, 4 July 2011, *Norsaengsri & Tathana 7940* (**QBG**); Doi Chong, Tham Luang-Khu Nam Nang Non FP, Mae Sai, 1309 m asl, 10 July 2012, *Norsaengsri & Tathana 9745* (**QBG**)]; Lamphun [Doi Kuhn Tan NP, 1250 m asl, 17 July 1993, *Maxwell 93-777* (**BKF, CMUB**)]; Lampang [Jae Sawn NP, 525 m asl,23 Aug. 1995, *Maxwell 95-544* (**BKF**); Ngao Dist., near Tham Pha Thai, 520 m asl, 24 Sept. 2008, *Middleton et al. 4582* (**BKF, E**)]; Uttaradit [Nam Pat, Phu Soi Dao NP, 680 m asl, 7 Aug. 2013, *Newman et al. 2622* (**QBG**)]; Tak [Chao Pho Phawo, 13 July 1999, *Newman 905* (**E**)]; Phitsanulok [Phu Soi Dao NP, Chat Trakan, 900 m asl, 25 July 2001, *Maknoi 171* (**QBG**); Nakorn Thai, Ban Nam Sai, Pha Lad Waterfall, 21 July 2001, *Maknoi 157* (**QBG**); Borpak, Phumiang-Phuthong WS, Chat Trakan, 420 m asl, 19 Aug. 2012, *Romklao Botanical Garden 0589/2555* (**QBG**)]; NORTH-EASTERN: Phetchabun [Thung Salaeng Luang NP, 600 m asl, 25 July 1966, *Larsen 893* (**E**)]; Loei [Phu Suan Sai NP, Na Haeo, route to Tadpa Waterfall, 11 July 2008, *Maknoi 2611* (**QBG**); Phu Suan Sai NP, Na Haew, 22 Aug. 2006, *Maknoi 1015* (**QBG**); Phu Suan Sai NP, Na Haew, route to Tadpa Waterfall, 11 July 2008, *Maknoi 2621* (**QBG**)]; EASTERN: Chaiyaphum [Near Ban Rai, 15° 34.704′N 101° 25.996′E, 440 m asl, 22 July 2013, *Mood & Vatcharakorn 3324* (**BKF**)]; Ubon Ratchathani [Korat, Kao Sisiket, Chan Tuk, 400 m asl, 1 Sept. 1924, *Kerr 9107* (**BKF**)]; Nakhon Ratchasima [Kao Soi Dao, 155 m asl, 21 July 2013, *Mood & Vatcharakorn 3316* (**BKF**)]; SOUTH-WESTERN: Kanchanaburi [Between Kritee and Mueng Chah, 1000 m asl, 9 July 1973, *Geesink & Phengkhlai 6209* (**BKF**); Thung Yai Naresuan WS, Lai Wo Subdist., 200–250 m asl, 17 June 1993, *Maxwell 93-654* (**BKF, CMUB**); Northwest of Tha Ka-nun, 14° 46.786′N 98° 34.682′E, 263 m asl, 21 Aug. 2011, *Mood & Vatcharakorn 3070* (**BKF**); East of Wang Krachae, 14° 16.887′N 98° 58.760′E, 100 m asl, *Mood & Vatcharakorn 3374* (**BKF**); Thong Pha Phum Dist., Maeklong Watershed Res. Station, 300 m asl, 24 Aug. 1999, *Wongprasert s.n.* (**BKF**); Thong Pha Phum NP, 900 m, 12 Aug. 2004, *Nielsen et al. s.n.* (**BKF**); Thong Pha Phum NP Summit Trail, 900 m asl, 22 Aug. 2004, *Nielsen 1867* (**BKF**); Sai Yok, 12 Dec. 1961, Larsen 8685 (C); Khao Yai, 9 Aug. 1968, *B.N. & S.P. 258* (**BKF**); Si Sawat Dist., Khao Po Teng, 900 m asl, 15 June 2001, *van de Bult 432* (**BKF**); Huai Lam Khut Ngu, Si Sawal, 7 July 1973, *Sutheesoen 2522* (**BK**); Si Sawat, 11 Aug. 1968, *Prayad 1498* (**BK**)]; Phetchaburi [Kaeng Kra Chan NP, on road to Thor Thip Waterfall trail entrance, July 2014, *Mood & Trisarasri 3464* (**BKF**)]; CENTRAL: Nakhon Nayok [Nang Rong Falls, 300 m asl,13 Aug. 1968, *Larsen 3365* (**AAU, BKF**); Nang Rong Falls, 16 Sept. 1972, *Maxwell 72-380* (**BK**); Muang Dist., Khao Yai NP, Mo Singto area, 770 m asl, *Chongko 124* (**BKF**); Muang Nakhon Nayok, Tambon Hin Tang, 1250 m asl, 23 Aug. 2012, *Middleton et al. 5647* (**E**); Near Mu Si, 21 July 2013, 14° 25.906′N 101 24.017′E, *Mood & Vatcharakorn 3316* (**BKF**)]; SOUTH-EASTERN: Chachoengsao [Wang Nam Yen, Sap Khanun, 19 July 1999, Newman 922 (**BKF, E**)]; Sa Kaew [near Pangsida NP, July 2013, *Mood & Vatcharakorn 3315/3316* (**BKF**)]; Chanthaburi [Kao Sabap, (no date, ca 1927), *Kerr s.n.* (**P, P01764010**); Kao Sabap, 6 July 1927, *Put 919* (**BK**); Pliew Waterfalls, Lam Sing Dist., 27 July 1969, *Maxwell s.n.* (**BK**); Lam Sing Dist., Pliew Waterfalls, 13 Aug. 1972, *Maxwell 72-314* (**BK**); Khao Khitchakut NP, Khao Phra Bat, 1020 m asl, 17 Aug. 2008, *Phonsena 6180* (**BKF**); Near Pliew Waterfalls, *Mood & Vatcharakorn 3282* (**BKF**)]; Trat [Huai Raeng Dong Maduae, ca 50 m asl, *Smitinand 1324* (**BK**); Ko Chang, 4 Sept. 1992, *Niyomdham 3209* (**BKF**); Ko Chang, sea level, 2 Aug. 1973, *Murata et al. T-17405* (**BKF**)]; PENINSULAR: Ranong [East of Khao Niwet, 09° 57.614′N 98° 39.993′E, 110 m asl, 24 Aug. 2011, *Mood & Vatcharakorn 3112* (**BKF**)]; Trang [Hat Chao Mai NP, Nam Ron Hot Spring area, 28 Aug.

1996, *Wilkin 807* (**BKF**)]; Songkhla [Ban Rainuea, Bahoy, Sabayoi, 100 m asl, 27 July 1999, *Maknoi T33* (**QBG**); Ban Rainuea, Bahoy, Sabayoi, 100 m asl, 25 July 2000, *Maknoi T91* (**QBG**)]; Yala [Betong, Pattani, 400 m asl, 1 Aug. 1928, *Kerr 7448* (**BK**); Betong area, July 2013, *Mood & Vatcharakorn 3309* (**BKF**)]. VIETNAM: Đak Nong Province: Draysap Waterfall, 380 m asl, 27 July 2009, *Trần et al. 160* (**E, SING** spirit**, VMN**).

Notes.— *Vegetative growth*. Once monsoonal rains commence in May, a succulent stem emerges from the ground. This growth can be from either a germinating seed, a mature bud-crowned tuberous root or the previous-year's aerial or subterranean bulbil. The growth of the plant is rapid, so that in ca 30 days it can become fertile. At the same time, the plant produces several to many subterranean stems along with numerous, thin, adventitious roots with rootlets from the base of the main above-ground stem. In areas where there is excellent soil, the mass of vegetative growth can become a tangle of intertwining axillary branches above ground with several branched stems below. The vegetative phase lasts 7–8 months.

Flowering. The inflorescence is distichous with bracts overlapping almost equally on both sides of the rachis. The flowering sequence occurs from the apex downward (basipetalous), one flower at a time (rarely two), opening in the early morning and senescing within 24 hours. New and old flowers overlap in timing and are frequently in juxtaposition. In the first hours the thecae dehisce dropping pollen on the labellum while still clasping the stamen. In the later part of the cycle, the thecae rotate radially, just enough to release the style. The stigma then reflexes slightly and exudes a large droplet of sticky, clear liquid. If the style arching is pronounced, it can touch the labellum where the dropped pollen has accumulate. Nothing is currently documented about natural pollinators, self-incompatibility or other aspects of sexual reproduction in this species. Flowering usually lasts about three months with both the main and axillary stems producing an inflorescence.

Sexual reproduction. Seeds are produced at various times during the flowering period, albeit sparsely. Once the seed capsule splits, the outer wall quickly disintegrates, allowing the seed to disperse. The scant white aril and capsule do not seem to provide an attractant for rodents or birds, although this vector is not totally dismissed. Based on several ex situ germination tests of wild seed harvested in August, germination never occurred before April the following year. This has also been the case in most other deciduous *Boesenbergia* seed germination tests (unpublished data, JDM).

Asexual reproduction. Bulbils have been observed to form on stems above and below ground. These propagules are composed primarily of adventitious root material and a small portion of old stem with a bud, similar to those of *Globba* L. species (Box & Rudall, 2006). The conditions required for propagule production are unknown as not all plants in all habitats are equally productive. As observed in the field and ex situ, it appears that physiological factors, combined with certain environmental conditions stimulate the adventitious, clonal material. In some cases, a long adventitious root will emerge from a main stem node, while on another part of the stem the adventitious material will form a bulbil. In either case, occurrence seems random. On some plants, bulbils will be formed just below the inflorescence, whereas none are produced on other parts. When the stem dies, the bulbil remains attached until the stem disintegrates. The remaining organ retains a precursory stem bud that, in the next season, will grow into a new plant given proper conditions. The underground propagules also start as an adventitious root, which initiates from the stem base as a "dropper" or "sinker", becoming long, fleshy, and tuberous during the growing season. When the stem dies, the long propagule retains a stem bud at the proximal end, distinguishing it from a true tuberous plant, e.g. *Solanum tuberosum* L. Another propagule shape occurs on underground stems produced from the main stem. These propagules are late to develop and normally only have enough time to become spherical before plant dormancy. After one or more years growth all propagules of the same age look very similar – fusiform to ca 25 cm long, white and covered with very short, fine rootlets. In each additional year of growth, the tuberous root further elongates and expands, often producing additional tuberous roots at the proximal end so that an older perennating organ can have four or more conjoined tuberous roots with a single proximal crown bud. No matter the number of these tuberous roots, only one stem will emerge from the bud in the new season.

var. ***major*** Mood & Veldk. **var. nov.**

Boesenbergiae parvulae (Wall. ex Baker) Kuntze affinis planta multo maiore 60–75 cm alta, inflorescentia maiore ca 15 cm longa, floris tubo ca 6.5 cm longo differt. TYPUS: *Mood 14P84*, Cultivated in Hawaii, USA, 1 Oct. 2014 (holo **BKF**; iso **AAU**). Originally from Thailand, Prachuap Khiri Khan Province, 110 26.915′N 990 25.136′E, 180 m asl., 23 Aug. 2011, *Mood & Vatcharakorn 3100*, cultivated as *M3100*. (Fig. 6, 8)

Differs in the plant to ca 75 cm tall, flowers to ca 6–6.5 cm long, labellum saccate, orbicular, ca 3 × 2.8 cm, white, throat spotted light or dark red in the centre, lateral staminodes obovate, ca 2.3–2.7(3) × 1.4–2 cm. Fruit not seen. Bulbils above and below ground, variable in size, up to ca 4 × 0.5 cm, externally green or white, internally white, surface covered with short rootlets, occurring in the leaf axils, at the base of the inflorescence or on subterranean stems. (Described from living plants of M3100.)

Distribution.— Western and Central Thailand.

Ecology.— Found in deciduous forest growing in soiled crevices on limestone outcrops. Very rarely found away from the outcrops in deeper soil amongst limestone boulders. On several occasions it was found on sandstone, in evergreen forest.

Phenology.— No pollinators observed. Flowering commences in early July and continues into November.

Etymology.— Named for its large size in comparison to the species.

Chromosome count.— 2n=20 (Mandakova, in ed.).

Additional specimens examined: THAILAND. NORTHERN: Lamphun [Li Dist., Mae Ping NP, Ko Luang Waterfall, 400 m asl, 9 Sept. 2009, *Middleton & Triboun 4822* (**BKF**)]; Tak [Mueang Tak Dist., Lan Sang NP, 700 m asl, 20 Apr 1985, *Niyomdham 901* (**BKF**)]; SOUTH-WESTERN: Kanchanaburi [Sai Yok, 31 July 1928, *Put 1792* (**BK**); Ka Tha Lai, 300 m asl, 2–4 June 1946, Kostermans 793; Wang pho, 15 Oct. 1967, *Chermsirivathana 783* (**BK**); Erawan NP, 400 m asl, 20 Nov. 1971, *Van Beusekom et al. 3884* (**BKF**); Sai Yok, Wangkamen, 200 m asl, 29 Jan. 2000, *Phengklai et al. 14085* (**BKF**); Sai Yok, Wangkamen, 200 m asl, 23 Sept. 2000, *Phengklai et al. 14010* (**BKF**); Sai Yok Dist., Mahidol Uni. campus, 200 m asl, 12 Augt. 2006, *Chongko 537* (**CMUB**); Huai Kayeng, Sai Yok, 21 Augt. 2011, *Mood & Vatcharakorn 3076* (**BKF**); Wang Badaan Cave, Augt. 2011, *Mood 3171* (**BKF**); Sai Yok, Tam Lawa, 70 m asl, 30 July 2013, *Mood & Vatcharakorn 3369* (**BKF**); Nong Kum, 147 m asl, 11 Augt. 2015, Mood & Harwood 3502]; Ratchaburi [Khao Kra Chom, 500 m asl, 18 Nov. 1995, *Niyomdham 4478* (**BKF**)]; Phetchaburi [Kaeng Kra Chan NP, 250–300 m, 3 Augt. 1995, *Larsen et al. 45378* (**AAU, QBG**); near Kaeng Kra Chan NP, 1 Augt. 2013, *Mood & Vatcharakorn 3375* (**BKF**)]; Prachuap Khiri Khan [Amphoe Thap Sakae, Huai Tang, 16 Oct. 1960, *Chandrapraseng 56.* (**BK**)*;* Kaeng Kra Chan NP, 250 m asl, 4 Aug. 1995, *Larsen et al. 45403* (**AAU**)]; SOUTH-EASTERN: Chonburi [Siracha Dist., Chundaten Falls, 800 m asl, 17 Aug. 1974, *Maxwell 74-820* (**BK**); Siracha Dist., Khao Kieo, 800 m asl, 27 June 1976, *Maxwell 76-410* (**BK**)].

Notes.— The notes under var. parvula also apply here. Further, this variety is easy to identify due to its 50 cm length/height normally achieved before flowering, large leaves, thick stems and preference for limestone outcrops. When the plants are fertile the identification is simplified further as the flowers are ca 4 times as large as var. parvula.

CONCLUSIONS

At the end of this five-year study of the four species, no major morphological differences could be ascertained that might be useful in distinguishing one from another. Only minor variations were found, that in the authors' opinion are not uncommon in these or other widely distributed *Boesenbergia* species (Table 1). As for the molecular phylogenetic results, tissue analyses of *B. gelatinosa*, *B. jahaiana*, and *B. parvula* showed a distinct lack of bootstrap support for any internal structure which might provide evidence that they are distinct species. Unfortunately, due to the age of samples of *B. phyllostachya* (*Trần et al. 160*), no usable data could be recovered for genetic comparison. Consequently, *Boesenbergia gelatinosa* and *B. jahaiana* are placed in synonymy with *B. parvula* based on the morphology and supporting phylogenetics, while *B. phyllostachya* is placed in the same synonymy based on its morphological similarities. The classification of *B. parvula* var. *major* is considered distinct based on its much larger size of the plant and flower which is readily apparent in the field and herbarium.

Table 1. Species Comparison

Character/Species	*Boesenbergia gelatinosa*	*Boesenbergia jahaiana*	*Boesenbergia parvula*	*Boesenbergia phyllostachya*
Type locality	W. Thailand	P. Malaysia	Myanmar	Vietnam
Soil derivation	Sandstone/Granite	Sandstone	Sandstone/limestone	Sandstone
Type forest	Evergreen to semi-deciduous	Evergreen	Evergreen to semi-deciduous	Evergreen to semi-deciduous
Elevation	300–600 m	300–600 m	50–1200 m	unknown
Perennating organ	Bud-crowned tuberous root	Bud-crowned tuberous root	Bud-crowned tuberous root	Bud-crowned tuberous root
Stem	Branched/succulent	Branched/succulent	Branched/succulent	Branched/succulent
Plant height	to 30 cm	30–50 cm	to 30 cm	30–50 cm
Sheaths	Reddish/corrugate	Red/corrugate	Red or green/ corrugate	Green/corrugate
Ligule	Triangular	Triangular	Triangular	Triangular
Lamina colour Dorsal/Ventral	Green-silver/red or green	Green/green	Green-silver/ red or green	Green/green
Labellum shape flattened	Orbicular	Orbicular	Orbicular	Orbicular
Labellum colour pattern	Red spotted throat, red streaked margin	Solid red, throat to margin	Spotted throat, solid red margin	Light red spotted throat, striped margin
Asexual propagules	Bulbils	Bulbils	Bulbils	Unknown

ACKNOWLEDGEMENTS

We would like to thank the, staff of BKF (Department of National Parks, Wildlife and Plant Conservation) for their continued assistance in the field and herbarium; P. Vatcharakorn and P. Chalermglin (Thailand) for their accompaniment in the field; Nyi Nyi Kyaw, Director General, Forest Department, and Taung Naing Oo, Director of Forest Research Institute, Forest Department, Myanmar; T. Mandakova (Central European Institute of Technology, Brno, Czech Republic) for chromosome counts; The Field Museum, Chicago USA (F) for use of Pritzker DNA Laboratory facilities; and Linda Ann Vorobik (Berkeley, USA) for the plate compositions.

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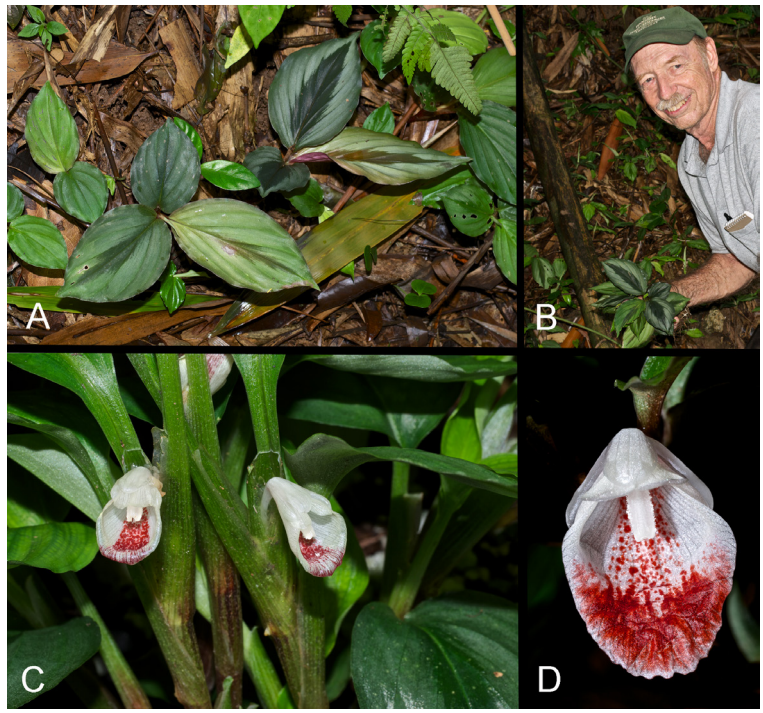

Figure 2. *Boesenbergia parvula* (Wall.) Kuntze: A. Plants near the type locality in Myanmar (*M3460*); B. JDM with plants near type locality in Myanmar; C. Fertile plants, Chiang Mai Province (*M3407*); D. Flower, Chiang Mai Province (*M3350*).

Figure 3. *Boesenbergia parvula* (Wall.) Kuntze: A. Flower, Ranong Province (*M3112*); B. Limestone habitat, Kanchanaburi Province; C. Flower, Yala Province (*M3309*); D. Fertile plant, Yala Province (*M3309*).

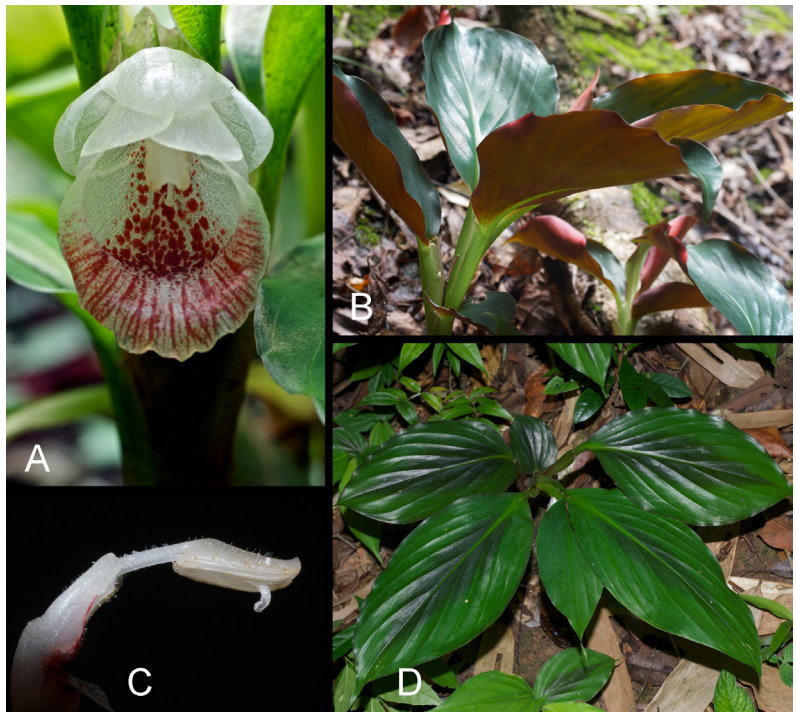

Figure 4. *Boesenbergia parvula* (Wall.) Kuntze: A. Flower, Chanthaburi Province (*M3282*); B. Juvenile plant, Chanthaburi Province, (*M3282*); C. Typical anther, Sa Kaeo Province (*M3316*); D. Juvenile plant, Sa Kaeo Province (*M3316*).

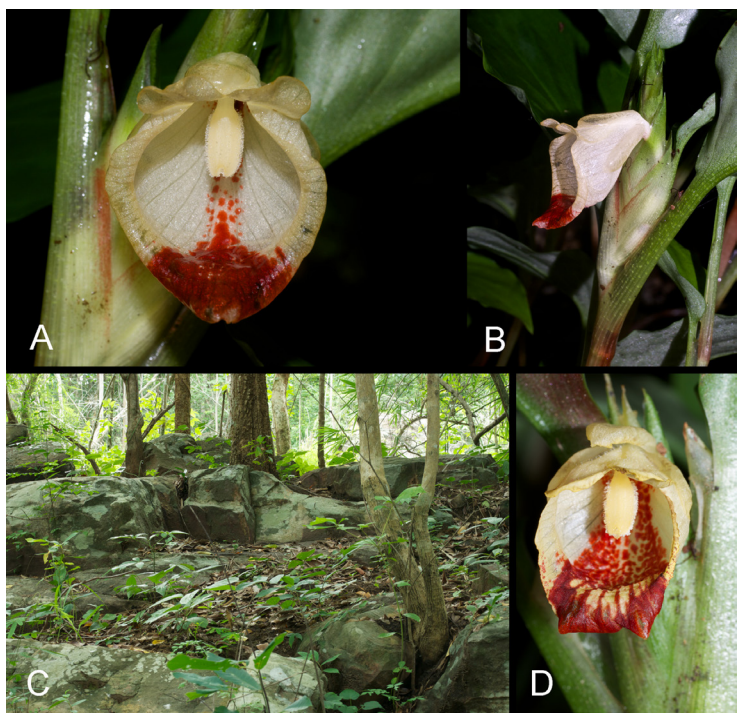

Figure 5. *Boesenbergia parvula* (Wall.) Kuntze: A. Flower, Louangphabang, Lao P.D.R. (*M3488*); B. Inflorescence with flower, Louangphabang, Lao P.D.R. (*M3488*); C. Habitat on sandstone, Chaiyaphum Province (*M3324*); D. Flower, Chaiyaphum Province (*M3324*).

Figure 6. Comparison of *Boesenbergia parvula* var. *major* Mood & Veldk. (left) with *B. parvula* (Wall.) Kuntze. (center & right); A. Lt.- *M3100*, Ctr.- *M3282*, Rt.- *M3070*; B. Lt.- *M3076*, Ctr.- *M3112*, Rt.- *M3100*; C. Lt.- *M3100*, Ctr.- *M3282*, Rt.- *M3070*; D. Lt.- *M3076*, Ctr.- *M3112*, Rt.- *M3100*.

Figure 7. *Boesenbergia parvula* (Wall.) Kuntze: A. Bud crowned tuberous root (perennating organ) Chiang Mai Province (*M3350*); B. Subterranean bulbils, Sa Kaeo Province (*M3316*); C. Seed capsules, Kanchanaburi Province (*M3374*); D. Aerial bulbils, Sa Kaeo Province (*M3316*).

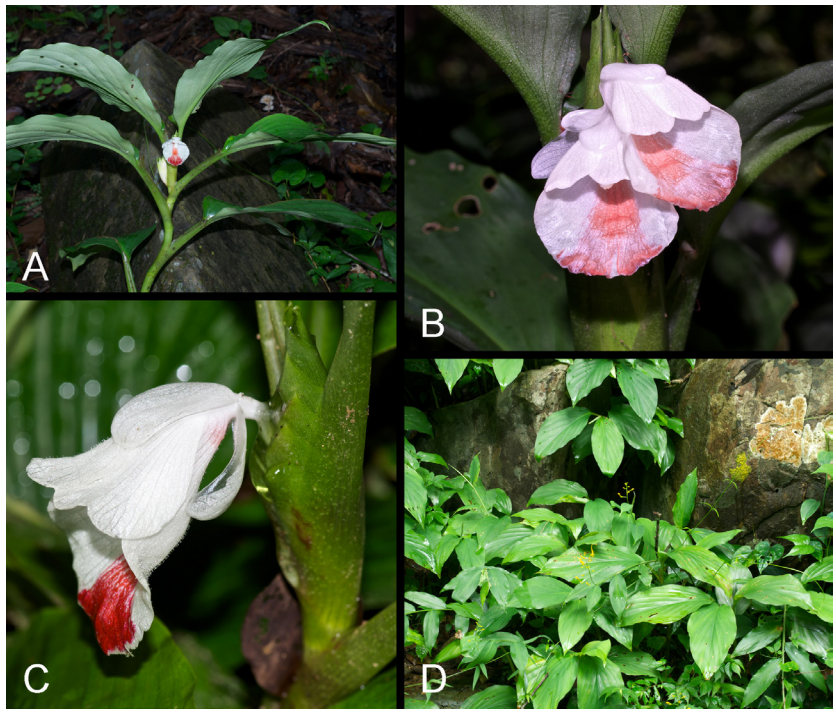

Figure 8. *Boesenbergia parvula* var. *major* Mood & Veldk.; A. Fertile plant, Phetchaburi Province (*M3375*); B. Flowers, Prachuap Khiri Khan Province (*M3100* type); C. Flower, Kanchanaburi Province (*M3076*); D. Plants on limestone outcrops, Kanchanaburi Province (*M3369*).

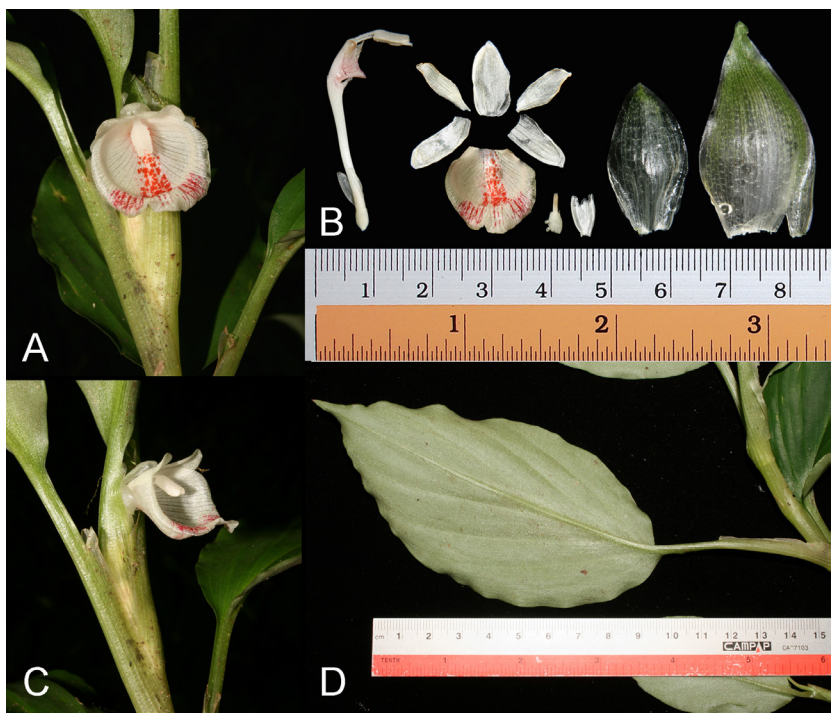

Figure 9. *Boesenbergia parvula* (Wall.) Kuntze. (*Trần et al. 160*, Vietnam); A. Flower; B. Dissection of flower with bract and bracteole; C. Flower; D. Stem and leaf.

Appendix 1. 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 parvula (Wall.) Kuntze:

M3070 (*Mood & Vatcharakorn 3070*, BKF) KX425630/KX432264

M3112 (*Mood & Vatcharakorn 3112*, BKF) KX425631/KX432265

M3282 (*Mood & Vatcharakorn 3282*, BKF) KX425632/KX432266

M3309 (*Mood & Vatcharakorn 3309*, BKF) KX425633/KX432267

M3315 (*Mood & Vatcharakorn 3315*, BKF) KX425634/KX432268

M3316 (*Mood & Vatcharakorn 3316*, BKF) KX425635/KX432269

M3324 (*Mood & Vatcharakorn 3324*, BKF) KX425636/KX432270

M3350 (*Mood & Vatcharakorn 3350*, BKF) KX425642/KX432271

M3460 (*Mood & Chalermglin 3460*, BKF) KX425638/KX432273

M3464 (*Mood & Trisarasri 3464*, BKF) KX425639/KX432274

M3472 (*Newman et al. 2622*, QBG) KX425640/KX432275

M3374 (*Mood & Vatcharakorn 3374*, BKF) KX425637/KX432272

M3488 (*Mood & Harwood 3488*, BKF) KX425641/KX432276

Boesenbergia parvula* var. *major Mood & Veldk.:

M3076 (*Mood & Vatcharakorn 3076*, BKF) KX425624/KX432258

M3100 (*Mood & Vatcharakorn 3100*, BKF) KX425625/KX432259

M3171 (*Mood & Vatcharakorn 3171*, BKF) KX425626/KX432260

M3369 (*Mood & Vatcharakorn 3369*, BKF) KX425627/KX432261

M3375 (*Mood & Vatcharakorn 3375*, BKF) KX425628/KX432262

M3502 (*Mood & Harwood 3502*, BKF) KX425629/KX432263

Boesenbergia pulcherrima (Wall.) Kuntze: *Mood 08P276* (BKF) JX992748/JX992809.

Boesenbergia rotunda (L.) Mansf. : *M1764* (*Mood 1764*, BKF) KX425623/KX432257

Boesenbergia xiphostachya (Gagnep.) Loes.: *M11C86* (*Mood 11C86*, BKF) KX425643/KX432277