A REVISION OF GAGNEPAINIA AND HEMIORCHIS (GLOBBEAE: ZINGIBERACEAE)

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The species of Gagnepainia K.Schum. and Hemiorchis Kurz are revised throughout their ranges. These genera are shown with evidence from morphological and molecular studies to be distinct, although closely related to each other. Two species of Gagnepainia and three of Hemiorchis are recognised. A key to the genera of Globbeae and keys to the species of Gagnepainia and Hemiorchis are given, all names are typified and descriptions are provided. Conservation assessments of all taxa are proposed.

Keywords. Gagnepainia, Hemiorchis, molecular phylogeny, Southeast Asia, taxonomic revision.

INTRODUCTION

The Zingiberaceae are pantropical herbs with their centre of diversity in tropical Asia. Fifty-seven genera are classified into four subfamilies: Zingiberoideae, Alpinioideae, Siphonochiloidae and Tamijioideae (Kress et al., 2002, plus new genera described since then). The Zingiberoideae, which are most easily characterised by the presence of large, petaloid lateral staminodes, are divided into two tribes, Zingibereae and Globbeae.

The three genera of the Globbeae, Gagnepainia K.Schum., Globba L. and Hemiorchis Kurz, are distinguished from the Zingibereae principally by a unilocular ovary with an incomplete axis such that the ovules are found towards the base of the ovary, and a long stamen filament that arches forwards over the labellum. Further morphological support for the tribe has been given by Benedict et al. (2015), who reported that the seven species of Globbeae they studied share a unique combination of 16 seed morphological characters.

Globba is by far the largest genus in the tribe, with an uncertain number of species, at least 80, distributed from Sri Lanka to Australia. Gagnepainia and Hemiorchis, by contrast, are much smaller, with three names each. These plants are small, deciduous, precociously flowering herbs occurring mainly in the forest understorey of the Indochinese Continental Region. Their distributions overlap near the border between Burma and Thailand. Hemiorchis ranges from the eastern Himalayas (eastern Nepal, Sikkim, Bhutan) south-eastwards through northeastern India and Bangladesh to Burma and northern Thailand. Gagnepainia ranges from Thailand to Laos and Cambodia.

Although the Globbeae are morphologically distinct from the remaining Zingiberoideae, the tribe was not well-supported in a phylogenetic analysis by Williams et al. (2004, p. 109,
This analysis, which included three accessions of *Gagnepainia* and four of *Hemiorchis*, sequencing internal transcribed spacer (ITS) and *matK* from each, found the two genera to be closely related as sister taxa and strongly supported as a monophyletic group. They share similarities in vegetative and floral characters that confirm this relationship (Table 1). In particular, the complex structure and ornamentation of the central region of the labellum is believed to be a unique and powerful unifying character of the two genera (Williams et al., 2004). Species delimitation and application of names in each genus remain largely unclear, however, so the aims of this work are to carry out a taxonomic revision using all available materials.

**Taxonomic History**

Kurz first established *Hemiorchis* with a single species, *Hemiorchis burmanica*, from Burma in 1873. In 1894, King added a second species from Sikkim, *Hemiorchis pantlingii* King. Baillon described three more species in 1895, *Hemiorchis godefroyi* Baill., *Hemiorchis harmandii* Baill. and *Hemiorchis thoreliana* Baill. from materials said to have been collected in Cambodia. He noted that these three species were unlike the type species, *Hemiorchis burmanica*, differing significantly in floral characters such as floral tube length and labellum morphology.

Schumann (1904), in the most recent worldwide monograph of the Zingiberaceae, described another species of *Hemiorchis*, *H. rhodorrhachis* K.Schum. This new taxon had been described and illustrated as *Hemiorchis burmanica* by J.G.Baker (1890, tab. 7120) from cultivated material at the Royal Botanic Gardens, Kew.

In the same work, Schumann (1904) also reconsidered Baillon’s three species of 1895, and noting that they all had elongate filaments and trilobed labella with narrow, linear median lobes, and lateral staminodes twisted at the base, erected the genus *Gagnepainia* K.Schum. Schumann’s combinations are *Gagnepainia godefroyi* (Baill.) K.Schum., *Gagnepainia harmandii* (Baill.) K.Schum. and *Gagnepainia thoreliana* (Baill.) K.Schum. *Gagnepainia* was last revised by Gagnepain (1908), and *Hemiorchis* was last revised by Schumann (1904).

Although the numbers of species in these genera are small, the identity of each species is unclear (Leong-Škorničková, 2009), and in some recent works, names have been applied interchangeably to the species, particularly in *Gagnepainia* (Phâm, 2000; Larsen & Larsen, 2006; Leong-Škorničková, 2009; Picheansoonthon & Tiyaworanant, 2010). A detailed study of the type materials is necessary in order to resolve this question.

**Materials and Methods**

Specimens or digital images of specimens were obtained from BK, BKF, CAL, CMU, E, K, L, P, U and US, which hold substantial collections from the Indochinese Continental Region, including type specimens cited in protologues. Eighty-one herbarium specimens of *Gagnepainia* were examined, 41 of them as digital images only. Forty-nine herbarium specimens of *Hemiorchis* were examined, 23 of them as digital images only. Additionally, living plants in the collection of the Royal Botanic Garden Edinburgh (RBGE) were studied (Table 2).
| Character                                | Globba                                      | Hemiorchis                                  | Gagnepainia                                  |
|------------------------------------------|---------------------------------------------|---------------------------------------------|----------------------------------------------|
| Inflorescence position                   | Majority arising terminally (rarely basally) on a shoot with leaf blades | Arising basally, separate from leafy shoots and before them | Arising basally, separate from leafy shoots and before them |
| Anther appendages                        | Usually present                            | Absent                                      | Absent                                       |
| Anther                                   | Hinged                                     | Not hinged                                  | Not hinged                                  |
| Lateral staminode attachment            | At or above the labellum                   | At or beside the labellum                   | At or beside the labellum                    |
| Filament                                 | Longer than anther, arched                  | Shorter than or equal to anther, slightly curved | Longer than anther, arched                  |
| Central keel(s) and apical projection(s) on labellum | Absent                                      | Present                                     | Present                                     |
| Labellum partially fused to filament or free? | Fused                                      | Free                                        | Free                                         |
| Floral tube reflexed or straight?        | Reflexed                                   | Straight                                    | Straight                                    |
| Leaf lamina                              | Terminating at apex of petiole             | Decurrent on petiole                        | Decurrent on petiole                        |
| Rhizome                                  | Many tuberous roots from a central rhizome | Long, narrow rhizomes lacking tuberous roots | Many tuberous roots from a central rhizome, tubers forming at the tips |
| Blooming period                          | Throughout or early rainy season           | Early rainy season and precocious           | Early rainy season and precocious           |
| Distribution                             | Throughout tropical Asia                   | E Himalayas (E Nepal, Sikkim, Bhutan), NE India (W Bengal, Meghalaya, Assam, Mizoram), Bangladesh, Burma and N Thailand  | Thailand, Laos and Cambodia (Vietnam – uncertain) |

* Modified from Williams et al. (2004, p. 102, Table 1).
Table 2. Materials from the RBGE living collection and National Center for Biotechnology Information GenBank

| Taxon                  | Source of material                      | Original collection locality | Voucher herbarium specimens (at E, unless otherwise stated) | GenBank accession number |
|------------------------|----------------------------------------|------------------------------|-------------------------------------------------------------|--------------------------|
| **Alpinia galanga**    | Cultivated at Smithsonian Institution   | Hawai’i (cultivated)         | *Kress & Bordelon* 94-5263 (US)                             | AF478715 AF478815        |
| **Boesenbergia rotunda** | Hawai’i (cultivated)                     | Thailand, Phitsanulok       | *Mood* M1764 (BKF)                                          | KY701331 KY701344        |
| **Curcuma rhambota**   | RBGE living accession 19991621A          | Laos, unknown locality       | *Škorničková 73331*                                        | JQ409854 JQ409658        |
| **Gagnepainia godefroyi** | RBGE living accession 19871253A          | Thailand, Chiang Mai         | *Newman 455, Newman & Škorničková 2014,*                      | MT269650 MT272822        |
| **Gagnepainia godefroyi** | RBGE living accession 20010444A          | Thailand, unknown locality   | *Tan* 15, 16                                                | MT269651 MT272823        |
| **Gagnepainia harmandii** | RBGE living accession 19991163A         | Thailand, Chachoengsao       | *Newman 1202, Newman & Škorničková 1468,*                    | MT269652 MT272824        |
| **Globba adhaerens**   | Wild collected                          | Thailand                     | *Williams 02-556 (DUKE)*                                    | AY339729 AY341099        |
| **Globba geoffroyi**   | Wild collected                          | Thailand                     | *Williams 00-387 (DUKE)*                                    | AY339692 AY341087        |
| **Globba insectifera** | Wild collected                          | China                        | *Williams 99-56 (DUKE)*                                     | AY339688 AY341080        |
| **Globba patens var. costulata** | Wild collected                                  | Malaysia, Pahang           | *Kato 10020 (TI)*                                           | AB049319 AB049274        |
| **Globba sessiliflora** | Cultivated at Smithsonian Institution   | Burma, Yangon                | *Kress 98-5613 (US)*                                        | AY339666 AY341096        |
| **Globba substrigosa** | Wild collected                          | Thailand                     | *Williams 02-602 (DUKE)*                                    | AY339722 AY341082        |
| **Globba wardii**      | Herbarium specimen                      | Burma, Chin State           | *Ward 22356 (BM, L)*                                        | AY339739 AY341102        |
| **Hemiorchis burmanica** | RBGE living accession 19871260A          | Thailand, Tak               | *Newman 861, Tan 8, 12*                                     | MT269653 MT272825        |
| **Hemiorchis rhodorrhachis** | RBGE living accession 19991652A       | Bangladesh, Chittagong      | *Newman 2452, Newman & Rahman 1001,*                        | MT269654 MT272826        |

*a* Taxa in bold have been newly sequenced in this study.
To manage all the data recorded from the specimens, information was added to the Zingiberaceae Resource Centre (continuously updated), an electronic database relating to Zingiberaceae that is maintained by the fifth author. The database is populated by the PADME system (Miller et al., 2015), which was developed at the RBGE. This revision has largely been put together using reports (e.g. annotations, citations of specimens studied in geographical sequence) generated by PADME. Mapping was done using the program DIVA-GIS (Hijmans, no date), based on geographical data downloaded from PADME.

Conservation assessments of the taxa were carried out according to the IUCN Red List Categories and Criteria, version 3.1, second edition (IUCN, 2012).

**Morphology**

The morphological species concept is adopted in this revision. Each species is defined by an assemblage of characters derived from observing and measuring herbarium specimens and living plants in cultivation.

Throughout the growing season of 2013, living plants at RBGE were observed from their emergence from dormancy through flowering and fruiting (achieved by hand pollination in some accessions), to new vegetative growth and dying back again late in the season. The flowers were dissected and observed under a binocular dissecting microscope, and the development and dehiscence of fruits of some plants were also observed and recorded. The roots, tubers, rhizomes and leafy shoots of mature plants were studied. During the growing season of 2019, further hand pollinations were carried out in order to produce fruits.

**Molecular Phylogeny**

The accessions sampled are listed in Table 2. Because all available sequences of Gagnepainia and Hemiorchis in the National Center for Biotechnology Information (NCBI) GenBank were either duplicates of those growing at RBGE or else poorly documented or not available to us, we decided not to use them and proceed only with material we have seen. Seven species of the closely related genus Globba, representing most sections, and three outgroup species, two from the subfamily Zingiberoideae (Boesenbergia rotunda (L.) Mansf. and Curcuma rhabdota Sirirugsa & M.F.Newman) and one from the subfamily Alpinioideae (Alpinia galanga (L.) Willd.), were included, i.e. sequences were downloaded from NCBI GenBank. Two regions were sequenced: ITS and matK.

A large-scale phylogenetic study of the Globbeae, especially Globba, is under way, and results will be published by the third author and colleagues in due course. The simple null hypothesis being tested here was that the species sampled do not fall into more than one clade, i.e. that Gagnepainia and Hemiorchis are one genus.

**DNA extraction and sequencing**

Total genomicDNAs were extracted using DNeasy Plant Mini Kits, available from Qiagen (Maryland, USA). Two regions were selected for amplification, namely nuclear ITS and
chloroplast matK. PCR amplifications of these regions were performed using BIOTAQ DNA polymerase from Bioline (London, UK), with bovine serum albumen as an enhancer. PCR products were purified using ExoSAP-IT, supplied by Affymetrix (California, USA), and sequencing reactions performed using the BigDye Terminator v3.1 Cycle Sequencing Kit from ThermoFisher Scientific (Massachusetts, USA). Sequencing primers were the same as the amplification primers. Samples were sent to Edinburgh Genomics (Edinburgh, UK) for sequencing. See the Appendix for the primers, PCR recipes and PCR profiles used. Raw sequences were assembled and edited using Sequencher 5.1 (Gene Codes Corporation, Michigan, USA).

Phylogenetic analysis

The alignment was made using MAFFT v.7.394 (Katoh & Standley 2013), then checked and improved manually in BioEdit v.7.0.4.1 (Hall, 1999). A partition homogeneity test (incongruence length difference, ILD, test; Farris et al., 1994) was performed in PAUP* 4.0 (Swofford, 2002). Nuclear regions were compared with chloroplast regions and easily passed the ILD test ($P = 0.93$). This result suggests that there is not a significant difference in the evolution of nuclear and chloroplast regions, and hence both may be concatenated and analysed together with partitioned analysis. The best evolution model of nucleotide substitution was computed using jModelTest 2.1.3 (Guindon & Gascuel, 2003; Darriba et al., 2012). The GTR+G and GTR+I model was selected as the best-fit model (based on AIC; Akaike information criterion) for the ITS and matK data set, respectively.

Two phylogenetic reconstruction methods with partitioned data set were applied.

1. Bayesian inference performed in MrBayes v.3.2.6 (Huelsenbeck & Ronquist, 2001, Ronquist & Huelsenbeck, 2003). The number of generations was set to 1,000,000, every 100th tree was sampled, and the first 25% of these trees were discarded as the burn-in.
2. Maximum likelihood (ML) analysis in RAxML v.8.2.10. (Stamatakis, 2014), with 20 starting trees generated by random addition and with 100 standard bootstrap replicates.

Results

Characters

Life form. All species of Gagnepainia and Hemiorchis are deciduous herbs. They are dormant during the dry season and sprout at the onset of the rainy season.

Root zone. Gagnepainia produces compact rhizomes, similar to those of many species of Curcuma and Zingiber (Fig. 1). Tuberous and feeder roots are produced from the rhizome. The tuberous roots are fleshy, each forming a swollen tuber at or near the apex later in the growing season.

Hemiorchis produces elongated, creeping, fleshy rhizomes, but no root tubers have been observed. In cultivated plants, the slender connections between the perennating sections of
rhizome break during the dry season and each disconnected section produces one or more buds, which grow into leafy shoots (Fig. 2).

**Pseudostems.** The laminae in both genera are decurrent onto the petiole. The ligule is a very short membranous structure at the junction of the leaf sheath and the petiole.

In *Hemiorchis*, the pseudostem shape, petiole morphology (length and shape), lamina shape and indumentum presence allow differentiation of the species. In *Gagnepainia*, there is little variation in vegetative structure between the species but there are some subtle characters by which they can be distinguished, namely the clasping of the basal leaf sheaths, the channelling of the petiole, the degree of folding of the plicate leaves, and the presence of an indumentum on the abaxial leaf surface.
Indumentum. An indumentum of simple hairs occurs on various parts of the pseudostems. Its presence and coverage vary and can occasionally be of taxonomic importance.

Inflorescences. Both Gagnepainia and Hemiorchis flower precociously at the beginning of the rainy season before any vegetative growth occurs, although in cultivated plants flowering may also occur after vegetative shoot growth has begun. The leafless inflorescence in both genera is a spike with sessile flowers borne spirally along an unbranched rachis. It arises directly from the rhizomes and the peduncle is covered initially by a few inflorescence sheaths exposing only the rachis. One to a few flowers open per day and last for only about a day. An indumentum is present on most parts of the inflorescence including the sheaths.
Kurz (1873) and King (1894) recorded bracts in *Hemiorchis burmanica* and *H. pantlingii*, respectively. Baker (1890) reported membranous, deciduous bracts in *Hemiorchis*, and Larsen *et al.* (1998) stated that each flower was subtended by a caducous bract. Larsen & Triboun (2000) mentioned that the inflorescences were either bracteate or ebracteate, and Singh *et al.* (2012) said the flowers could be ebracteate or with bracts to c.1 mm long. Floral bracts were observed only in a single photograph from the Smithsonian Institution and on one specimen from Kew (K000649571) during this revision. They seem to occur rarely in *Hemiorchis* but never in *Gagnepainia*.

**Flowers.** The calyx of *Hemiorchis* is more or less infundibuliform with three equal or subequal teeth 1/4 to 1/3 the length of the calyx and shorter than that of *Gagnepainia*, which is tube-like with lobes 1/3 to 1/2 the length of the calyx.

In *Gagnepainia* (Fig. 3A,B) and *Hemiorchis* (Fig. 3C), the floral tube is slender and narrow, surrounded by the calyx tube. The apex of the floral tube opens into a chamber to which the remaining perianth parts are attached. This is the floral chamber, which has not been described in detail before. We hypothesise that the floral chamber serves as a collection area for nectar, which in both genera is produced from a pair of epigynous nectaries at the base of the floral tube.

The staminodes in both genera are petaloid and are attached at the same level as the labellum and laterally to it. At the base of each staminode is a gland-like appendage that is situated at the sides of the opening to the floral chamber. In *Hemiorchis*, these appendages are more or less triangular and flap-like, whereas those of *Gagnepainia* are larger and more pronounced.

The corolla lobes of *Gagnepainia* reflex distinctively at anthesis, whereas those of *Hemiorchis* are generally flat with involute margins. The labellum in *Hemiorchis* is shallowly dish-like or deeply cymbiform with a mid-region of one or two keels that end as apical projections of the labellum. In *Gagnepainia*, the labellum is a more complex structure with two wing-like side lobes, a channelled mid-region and the apex adorned with 5 or 3 distinct projections.

In *Hemiorchis*, the androecium is made up of a short and slightly curved filament bearing the more or less rectangular anther, which has a shortly recurved apex. The androecium of *Gagnepainia* is made up of a long and arching filament connecting the lanceoloid anther with a more or less tapering apex.

The ovary in both genera is more or less ovoid to oblong, larger on the lower flowers, smaller and globose on the upper ones. It is densely puberulous with longitudinal grooves that become obvious as the ovary develops, and parietal placentation.

**Fruits.** The fruits of both genera are thick-walled capsules that are variously grooved and shortly puberulous. The calyx is persistent at the apex of the capsules, and the remaining perianth parts may be present as shrivelled remnants. There are preliminary indications that the direction of dehiscence differs between the two genera, but there is not sufficient evidence at present to allow a definite conclusion. Results obtained in the 2013 growing season seemed to show that in *Hemiorchis* the capsules dehisced apically, the pericarp
Fig. 3. Dissected flowers of Gagnepainia and Hemiorchis: A, Gagnepainia godefroyi (drawn from Tan 17 (E)); B, Gagnepainia harmandii (drawn from Tan 13 (E)); C, Hemiorchis rhodorrhachis (drawn from Tan 10 (E)). For each species: a, front view, calyx removed; b, lateral view with calyx; c, lateral view with partial dissection to show floral chamber and extent of stylar enclosure; d, transverse section of floral tube at level of floral chamber, showing extent of stylar enclosure; e, transverse section of floral tube at mid-level, showing extent of stylar enclosure.
splitting into three valves from apex to base. Some seeds remained attached to the valves while others fell. The valves were brittle and also soon fell. By contrast, in *Gagnepainia* dehiscence seemed to occur basally, the capsule splitting into three valves from base to apex and remaining weakly connate as a united, brittle pericarp. The split pericarp soon fell, leaving the seeds attached to the three placentae that remained on the inflorescence.

Hand pollinations carried out in 2019 did not result in ripe fruits, so it is not yet possible to be confident that this is a useful character to separate the genera.

Thirteen seeds in a capsule of *Gagnepainia harmandii* (RBGE 19991163A) was the highest number recorded, of nine capsules obtained by hand pollination of three *Gagnepainia* accessions (RBGE 19991163A, 3 capsules; 20010444A, 3 capsules; 19871253A, 3 capsules) and three capsules from one *Hemiorchis* accession (RBGE 19991652A). The small, smooth seeds of both genera are obovoid to globose, light to dark olive-green in colour, and each with a short neck at the base that attaches to the placenta. Each seed is covered by 1/3 to 1/2 from the base by a white, veil-like aril.

**Molecular phylogeny**

The results of our phylogenetic analysis (Fig. 4) show that *Gagnepainia* and *Hemiorchis* are sister taxa that form a clade with 100% support in both Bayesian and ML analyses.
Individually, *Gagnepainia* and *Hemiorchis* are monophyletic, each with 98–100% support in both analyses. These results confirm those of Williams *et al.* (2004) but with improved statistical support. Within the *Gagnepainia* clade, the two samples of *Gagnepainia godeffroyi* form a strongly supported clade.

When rooted with *Alpinia*, the *Gagnepainia–Hemiorchis* clade clusters with the *Globba* clade to make the tribe Globbeae (Kress *et al.*, 2002), but the support for this clustering is quite low (38% posterior probability in Bayesian analysis, 38% ML bootstrap). Only adding more sequence data in a future study can prove or disprove the monophyly of this tribe.

**SYSTEMATIC TREATMENT**

*Key to the genera of Globbeae*

1a. Rhizome with finger-like tuberous roots; lamina not decurrent onto petiole; inflorescence a thyrse with cincinnate branches, terminal on pseudostem, rarely on a separate leafless shoot and then composed of cincinni; bracts showy and overlapping or greatly reduced to absent; floral tube conspicuously reflexed; labellum fused to floral tube, bifid or bilobed, rarely emarginate, lacking central point or lobe; filament long and arching, anther basifixed, hinged at junction with filament, with lateral appendages (except subg. *Mantisia*); fruit usually globose and rugose (elongate, ridged in sect. *Nudae*) __________________________________________________________ *Globba*

1b. Rhizome either long, irregular, without tuberous roots or tubers, or short and regular with tuberous roots bearing swollen tubers towards tips; lamina decurrent onto petiole; inflorescence spicate, cincinnate branches lacking, borne on a leafless stem; bracts absent or, if present, curved, subulate; floral tube straight; labellum free from floral tube, with a narrow central point or lobe; anther basifixed, not flexing at junction with filament, without lateral appendages; fruit ovoid-elliptic with numerous longitudinal ridges ___________________________________________________________ 2

2a. Rhizome short, with numerous tuberous roots and tubers towards tips; individual plant generally of multiple pseudostems; flowers generally white with light yellowish orange to orange or green with light yellowish green, lacking red or reddish brown colouring; corolla lobes tightly rolled up at anthesis, margins not involute; labellum fishtail-shaped or semilunar with two flat side lobes and a channelled mid-region ending in 5 or 3 distinct apical projections; filament long in proportion to flower, much longer than labellum; tip of anther acute; fruit a thick-walled capsule, more or less elongate or ovoid ___________________________________________________________ 1. *Gagnepainia*

2b. Rhizome long, creeping, brittle, without tuberous roots and tubers; individual plant generally of single pseudostems; flowers mostly light creamy brown to brownish pink (with or without pink, light yellow or orangey yellow); corolla lobes flat, reflexed, never coiled at anthesis, margins more or less involute; labellum deeply cymbiform with central ridge(s) and apical projection; filament short in proportion to flower,
clearly shorter than labellum; tip of anther truncate to emarginate; fruit a thick-walled capsule, more or less ellipsoid

2. Hemiorchis

1. Gagnepainia K.Schum., Pflanzenr. IV, 46 (Heft 20): 129 (1904); Gagnepain, Fl. Indo-Chine 6(1): 41 (1908); Larsen et al., in Kubitzki (ed.), Fam. Gen. Vasc. Pl. 4: 488 (1998); Larsen & Larsen, Gingers of Thailand 100 (2006); Leong-Škorničková, Gardenwise 32: 31 (2009); Picheansoonthon & Tiyaworanant, J. Roy. Inst. Thailand 2: 91 (2010). – Type: Gagnepainia godefroyi (Baill.) K.Schum., designated here.

Deciduous and precocious understorey herbs to 70 cm tall, erect, individual plant usually with multiple pseudostems. Rhizomes short and compact, formed right at the base of each plant, white when young, light brown to brown when old. Tuberous roots formed at the base of rhizomes, fleshy and rounded, white when young, light to dark brown when old. Tubers swollen, borne towards the tip of old tuberous roots, exterior light to dark brown, interior lighter. Feeder roots fine and numerous, white when young, light to dark brown when old. Pseudostems arising with plane of distichy of leaves parallel to rhizomes, more or less rounded to oval, with 2–5 basal leaf sheaths, pale to light green, longitudinal venation distinct, puberulous, indumentum present along sheath margins. Petioles long with recurrent lamina, open with undulating wings or narrowly channelled. Ligule perpendicularly encircling the inner circumference of the base of each petiole, very short and membranous, puberulous or shortly puberulous, almost translucent to tinged with a light faint brown. Leaves 3–11 on each pseudostem, alternate, lanceolate to broadly lanceolate, strongly or weakly plicate, adaxially light green to green or light to dark greyish green, indumentum present along leaf venation, sparse on lamina, abaxially a contrasting light greyish to silvery green, puberulous or glabrous, base attenuate to more or less obtuse, apex attenuate, margins entire. Inflorescence a spike to 51 cm tall, erect, with 2–6 basal inflorescence sheaths, finely puberulous, pale to light green, longitudinal venation distinct, inflorescence pale to light green, darker at peduncle and lighter at rachis, finely puberulous. Flowers: basal ones arranged in a spiral and subsequently in whorls or spirally arranged, sessile, zygomorphic, opening successively. Calyx tubular, 3-lobed, divided up to 1/2 of calyx tube length, pale whitish green or light green, finely puberulous, persistent in fruit. Floral tube straight and slender, as long as or longer than calyx tube, off-white to light greenish yellow or light green. Floral tube chamber infundibuliform, attached directly from the base to floral tube, off-white to light green. Corolla oblong, dorsal lobe larger than or equal to lateral lobes, tip obtuse, rolled up when flowers open, light yellowish or light green, adaxial shortly puberulous, abaxial glabrous. Lateral staminodes petaloid and wing-like, obliquely obovate, flat or reflexed with a thickened upper margin and protruding appendage present at the base, white with light yellowish orange to orange and an olive-green to yellowish brown spot on each basal appendage or light yellowish green to green and glistening white basal appendage. Labellum a complex structure, fish-tail-like or semilunar shape with two flat side lobes and a channelled mid-region ending in 5 or 3 distinct apical projections, side lobes are more or less squarish with two rounded angles at the margin or are almost semicircular with recurved apical margin, mid-region an open
channel leading down to floral chamber with no basal appendage, bordered on each side by a raised keel adjoining the side lobes, apex of labellum comprising 5 (2 vertical : 3 horizontal) or 3 (2 vertical : 1 horizontal) distinct projections, most of labellum white to off-white with bright yellowish orange to orange apex or side lobes light yellowish green to green with mid-region and apex glistening white. Stamens long, arching and glabrous, filament longer than anther, anther largely lanceoloid with more or less tapering apex, thecae narrowly lanceolate tapering at both ends and exserted, pollen yellow. Ovary elliptic or oblong to globose, pale to light green, longitudinal grooves unclear or up to c.8 and densely puberulous, tricarpellate, unilocular, placation parietal; epigynous glands 2, subulate; style single, filiform; stigma clavate to globose, exserted from apex of anther between thecae. Fruit a thick-walled capsule, more or less elongate or ovoid to oblong-ovoid and slightly flattened, appearing almost bifacial, with persistent calyx and remaining perianth shrivelled, pale to light green, finely puberulous, dehiscing into three valves. Seeds obovoid to globose, attached to placentae by a short neck, light green to light olive green and smooth. Aril translucent white, veil-like and covering 1/3 to 1/2 of seed.

Distribution. Two species occurring in Thailand, Laos and Cambodia. Perhaps also in Vietnam.

Ecology. Typically growing in partly shaded to shady understorey of bamboo, hardwood, deciduous or mixed evergreen forest, often growing along streams and seasonal streams, and in association with granite, shale or limestone substrate, 60–1000 m altitude. Occasionally remaining in disturbed, fire-damaged or degraded vegetation.

Key to the species of Gagnepainia

1a. Petiole open with more or less undulate wings; leaves 5–11, strongly plicate, abaxial surface more or less puberulous; flowers mostly white with light yellowish orange to orange; labellum fishtail-shaped, side lobes more or less square with two rounded angles at margin, labellum apex with 5 (2 vertical : 3 horizontal) projections ___________________________ 1.1. G. godefroyi

1b. Petiole more or less narrowly channelled, wings not undulate; leaves 3–7, weakly plicate, abaxial surface glabrous; flowers mostly green with light yellowish green; labellum semilunar, side lobes almost semicircular with recurved apical margin, labellum apex with 3 (2 vertical : 1 horizontal) projections _________________________ 1.2. G. harmandii

1.1. Gagnepainia godefroyi (Baill.) K.Schum., Pflanzenr. IV, 46 (Heft 20): 130 (1904); Gagnepain, Fl. Indo-Chine 6(1): 41 (1908); Leong-Škorničková, Gardenwise 32: 31 (2009). – Hemiorchis godefroyi Baill., Bull. Mens. Soc. Linn. Paris 2: 1196 (1895). – Type: Laos, Khammouane, Tha Khèk, 1875, A. Godefroy-Lebeuf s.n. (lecto P, barcode P032684, designated here; syn P, barcodes P032685, P00686499, P00686500). Figs 3A, 5.
Gagnepainia thoreliana auctt. non (Baill.) K.Schum., K.Larsen & S.S.Larsen, Gingers of Thailand 100 (2006); Picheansoonthon & Tiyaworanant, J. Roy. Inst. Thailand 2: 91 (2010).

Plants to 70 cm tall; basal leaf sheaths 2–4, alternate, margins not overlapping, open and tightly clasping, apex shortly tapering, pale to light green, paler or white at base, shortly puberulous, denser and longer on margin. Petiole 4–9.5 cm long, upper ones longer, openly channelled with more or less undulating wings. Ligule puberulous, translucent to tinged with faint brown. Leaves 5–11, strongly plicate, 10–39 × 6–13 cm, adaxially light green to green, whitish hirsute in 2 rows along secondary veins, more or less sparsely puberulous on lamina, denser along veins parallel to the margin, abaxially light greyish to silvery green, more or less puberulous to puberulous. Basal inflorescence sheaths 2–6, alternate, overlapping but not fused, apex shortly tapering, light green, basally paler, puberulous. Inflorescence 7.5–38.5 cm long, pale to light green, puberulous. Flowers: basal ones arranged in a spiral and subsequently in whorls, each whorl comprising a compact spiral of up to 5 flowers. Calyx 0.9–1.7 × 0.2–0.3 cm, divided up to 1/2 of calyx tube length, apex more or less obtuse, off-white to pale whitish green, puberulous. Floral tube 1.2–1.7 cm long, off-white to light pale greenish yellow. Floral tube chamber 0.2–0.3 × 0.1–0.15 cm, off-white to light pale greenish yellow. Corolla dorsal lobe c.1 × 0.4 cm, lateral lobes c.0.9 × 0.3–0.4 cm, apex obtuse, pale to light yellowish green, almost translucent towards margin. Lateral staminodes obliquely obovate, flat with thickened upper margin,

Fig. 5. Gagnepainia godefroyi, RBGE accession 19871253A. A, Open flowers; B, inflorescence. (Photographs: J. Leong-Škorničková.)
0.5–0.7 × 0.2–0.4 cm, white with light yellowish orange to orange, darker at thickened margin, basal appendage protruding, c.0.1 × 0.1 cm, each with an olive green to yellowish brown spot. Labellum fishtail-shaped, c.0.7–1 × 0.4–0.5 cm, mid-region an opening to the floral chamber, white to off-white, side lobes flat, more or less squarish with two rounded angles at the margin, apex of the labellum comprising 5 distinct projections: 2 vertical ones straight to slightly bent, like a pair of horns, white to off-white, 3 horizontal ones straight, perpendicular to the vertical pair, 2 shorter ones at base of vertical pair with 1 longer one in the middle, bright yellowish orange to orange. Stamen: white to off-white; filament 0.7–1 cm; anther 0.25–0.4 cm. Ovary 0.1–0.6 × 0.1–0.3 cm, pale to light green, longitudinal grooves obscure, densely puberulous; nectaries c.0.4 × 0.05 cm long; style 2.35–3.8 cm long; stigma c.0.05 × 0.05 cm. Fruit ovoid to oblong and slightly flattened, appearing almost bifacial, 0.5–4 × 0.3–1.7 cm, pale to light green, finely puberulous.

**Etymology.** Alexandre Godefroy-Lebeuf (1852–1903), French plant collector.

**Distribution.** Laos and Thailand (Fig. 6).

**Habitat and ecology.** 230–1000 m altitude.

**Proposed IUCN status.** Least Concern (LC). Area of occupancy (AOO) = 108 km², extent of occurrence (EOO) = 222,017 km². This taxon is common and widespread, and many of the collections were made near or within protected areas across its range.

**Specimens examined.** Unknown locality. Anon s.n. (barcode P06136208, P).

Laos. Khammouane: Tha Khèk, 1875, Godefroy-Lebeuf, A. s.n. (lecto P, barcode P032684; syn P, barcodes P032685, P00686499, P00686500); ibid, 1866–1868, Thorel, C. s.n. (P). Xaignabouly: Paklay, 1866–1868, Thorel, C. s.n. (P, 2 sheets).

Thailand. Unknown locality, acc. no. 1 vouchered as 23 v 2001, Kress, W.J. & Bordelon, M.W. 01-6976 (US). Bueng Kan: Si Wilai, Phu Thok, 12 v 2015, Puadja, P. 1871 (BKF). Chiang Mai: 25 ii 1957, Khantchai 358 (BKF); Chiang Dao, Ban Arunothai, Kio Pha Wok customs post, 13 v 2007, Pooma, R., Karaket, P., Pattharaaruntrcin, N. & Sirimongkol, S. 6731 (BKF); Doi Chiang Dao, 7 vi 1952, Garrett, H.B.G. 1382 (K); ibid, Mae Na Lao drainage, 18 iv 1950, Garrett, H.B.G. 1314 (K, 2 sheets); ibid, 8 iv 1989, Maxwell, J.F. 89-431 (BKF, CMU); ibid, 20 iv 1989, Maxwell, J.F. 89-486 (BKF, CMU); Doi Suthep-Pui National Park, 29 iv 1966, Chermisrivathana, C. 601 (BK); ibid, 1 v 1909, Kerr, A.F.G. 615A (BM, E, K); ibid, 23 v 1910, Kerr, A.F.G. 615B (E, K); ibid, 20 iv 1988, Maxwell, J.F. 88-491 (CMU); ibid, 28 iv 1988, Maxwell, J.F. 88-540 (CMU, E); ibid, Wat Fai Hin, 16 2007, Nuntawong, N. 7 (CMU); Mae Taeng, 25 iv 1929, Winit 718 (BKF, K).

Chiang Rai: Doi Tham Tu Pu, 9 v 1926, Garrett, H.B.G. 283 (K). Kanchanaburi: Huai Dong Wi, 5 iv 1992, Santisuk, T. et al. s.n. (BKF); ibid, 5 v 1992, Santisuk, T. et al. 270 (BKF); Khao Ta Mong, 9 iv 1965, Chantamuk, A. 1011 (BK, 2 sheets); Thong Pha Phum, 11 v 2003, van de Bult, M. 652 (CMU). Lampang: 8 v 1954, Bunyaratabhand, A. 25 (BKF); Chae Son National Park, 22 iv 1996, Maxwell, J.F. 96-559 (BKF, CMU); ibid, 29 iv 1996, Maxwell, J.F. 96-649 (BKF, CMU); ibid, along Mae Mon, below Chae Son waterfall, 10 iv 1996, Panatkool, M. 5 (CMU); ibid, 11 v 1996, Panatkool, M. 6 (CMU); Doi Luang National Park, Wang Nuea, Wang Kaew waterfall, 21 iv 1997, Maxwell, J.F. 97-366 (BKF, CMU). Lamphun: Doi Khun Taan National Park, 30 iv 1994, Maxwell, J.F. 94-571 (BKF, CMU). Loei: Phu Luang, 16 iv 1968, Chermisrivathana, C. 903 (BK). Nong Bua Lamphu: Na Wang, Ban Tham Erawan, 18 iv 1999, Kress, W.J. et al. 99-6315 (US). Phayao: Doi Luang
National Park, N of Cham Pa Thong waterfall, 29 iv 1998, Petrmit, O. 289 (CMU). Phitsanulok: 16 vi 1967, Phusomsaeng, S. 237 (BKF); Wang Thong, Kaeng Sopha, 27 vi 1967, Phusomsaeng, S. 256 (BKF); Thung Salaeng Luang National Park, 27 iv 1961, Chantamuk, A. s.n. (K); 27 iv 1961, Chantamuk, A. 797 (BKF). Phrae: Wang Chin, Ban Muang Kham, 15 iv 1970, Smitinand, T. & Cheke, A.S. 10795 (BKF). Tak: Lan Sang National Park, 29 v 1973, Geesink, R. et al. 5526 (BKF, E, L); Amphoe Muang, Doi Musoe, 8 v 1976, Sutheesorn, S. 3757 (BKF).

Cultivated at RBGE. Originally from Thailand, Chiang Mai, Mae Suai District, 19°44′N, 99°24′E, RBGE living collection accession number 19871253A: 3 viii 1993, Newman, M.F. 455 (E); 8 v 2006, Newman, M.F. & Škorničková, J. 1469 (E); 9 v 2007, Newman, M.F. & Škorničková, J. 2014 (E, 2 sheets); 9 viii 2013, Tan, W.M.S. 9 (E); 25 v 2013, Tan, W.M.S. 17 (E); date unknown, Tan, W.M.S. 18 (E); originally from Thailand, unknown locality, RBGE living collection accession number 20010444A: 1 v 2013, Tan, W.M.S. 15 (E); 23 v 2013, Tan, W.M.S. 16 (E).
Gagnepainia godefroyi is a distinctive species that appears to be the more common and widespread of the two species of this genus. It is characterised by its small, white flowers with light yellowish orange to orange markings, fishtail-shaped labellum with two flat lateral lobes that are rather square with two rounded angles at the margin, the mid-region of the labellum being an open channel leading to the floral chamber, and the apex of the labellum adorned by 5 (2 vertical and 3 horizontal) distinct projections that are white (the 2 vertical ones) and bright yellowish orange to orange (the 3 horizontal ones). When in bloom, it can easily be distinguished from the other species, Gagnepainia harmandii, which has mostly green flowers and different floral structures. The two species may be confused when not in bloom, because they are similar in vegetative morphology, requiring closer examination to tell them apart. Vegetatively, Gagnepainia godefroyi differs from G. harmandii by having tightly clasping basal leaf sheaths, openly channelled pedioles with undulating wings, and strongly plicate leaves with puberulous abaxial surfaces making them more or less velvety to touch. By contrast, Gagnepainia harmandii has basal leaf sheaths that are up to half or apically free from the pseudostem, narrowly channelled pedioles without undulating wings, and weakly plicate leaves that are glabrous on the abaxial surfaces and more or less leathery to touch. By these characters, it is possible to tell the two species apart even when they are not in bloom.

Baillon, in the protologue (Baillon, 1895), stated that he had abundant material of one species, which came, he said, from the “Montagne de Lakhon”. This is all the locality information to be found in the protologue. When Schumann (1904) made the combination in Gagnepainia, he repeated this information although with a misspelling in the place name, as follows, “Berge bei La-Khou (Godefroy in Expedition Harmand)”. On examination of the material at P, we found four sheets which match the protologue.

1. Godefroy s.n. (barcode P032684). Six plants in flower are mounted on this sheet, along with more flower material in a capsule. A label at the bottom left of the sheet bears the name ‘Hemiorchis godefroyi’ and the place name ‘Mont. de Lakhon’ in Baillon’s hand. ‘Cambodge’ is written in an unknown hand on the printed label at the bottom right of the sheet.
2. Godefroy s.n. (barcode P032685). This sheet consists of an envelope with many detached flowers in it, plus three sheets of handwritten description of the species and two sheets of line drawings. At the bottom right of the sheet is a label bearing the name ‘Gagnepainia godefroyi K.Sch.’
3. Godefroy s.n. (barcode P00686499). This sheet bears eight mounted plants and a number of loose plants in a capsule. The plants bear inflorescences but no flowers. The label indicates that the material was collected by Godefroy in 1875 at ‘Mont. de La Khon, Cambodge’. The same label bears the name ‘Hemiorchis godefroyi H. Baillon’, apparently in Gagnepain’s hand.
4. Godefroy s.n. (barcode P00686500). This sheet bears seven mounted plants at early fruiting stage. The label information is as on sheet P00686499.
There seems little doubt that the material on these sheets was collected by Godefroy, but the evidence that they form a single gathering (Turland et al., 2018; Art. 8) is weak. Sheets 1, 3 and 4 all state that the material was collected in Cambodia, but Lakhon is, in fact, the old name for the town of Nakhon Phanom, Thailand, and for the lands around it, on both sides of the River Mekong. A map in Harmand (1994, pp. 114–115) shows the “Province de La-Khon” stretching across the River Mekong. There are no mountains in Nakhon Phanom of Thailand (although the name means ‘Hill City’), but there are limestone mountains on the Laotian side of the river in the provincial capital of Khammouane, Tha Khèk. It seems likely that Godefroy collected his material in Khammouane Province of Laos rather than Nakhon Phanom Province of Thailand.

The sheet with barcode number P032684 clearly bears the name ‘Hemiorchis godefroyi’ in Baillon’s hand and shows the characters of the species in flower. It is the most suitable of the original materials to serve as lectotype. Sheets 2, 3 and 4 described above cannot be shown conclusively to form part of a single gathering with the lectotype, so they remain syntypes.

It should be noted that two recent publications have illustrated Gagnepainia godefroyi under the name G. thoreliana (Larsen & Larsen, 2006, p. 100; Picheansoonthon & Tiyaworanant, 2010, Figs 3, 4). Likewise, the photographs labelled Gagnepainia godefroyi in these two publications (Larsen & Larsen, 2006, pp. 101 and 102; Picheansoonthon & Tiyaworanant, 2010, Figs 1, 2) are of G. harmandii.

1.2. Gagnepainia harmandii (Baill.) K.Schum., Pflanzenr. IV, 46 (Heft 20): 129 (1904); Gagnepain, Fl. Indo-Chine 6(1): 41 (1908); Leong–Škorničková, Gardenwise 32: 31 (2009). – Hemiorchis harmandii Baill., Bull. Mens. Soc. Linn. Paris 2: 1196 (1895). – Type: Cambodia, unknown locality, 1875, A. Godefroy-Lebeuf (lecto P, barcode P032686, designated here). Figs 3B, 7.

Hemiorchis thoreliana Baill., Bull. Mens. Soc. Linn. Paris 2: 1196 (1895). – Gagnepainia thoreliana (Baill.) K.Schum., Pflanzenr. IV, 46 (Heft 20): 130 (1904); Gagnepain, Fl. Indo-Chine 6(1): 41 (1908). – Type: Cochinchine [southern Vietnam], 1862–1866, C. Thorel (lecto P, barcode P032687, designated here).

Gagnepainia godefroyi (Baill.) K.Schum. auct. non (Baill.) K.Schum.; Larsen & Larsen, Gingers of Thailand 101, 102 (2006); Picheansoonthon & Tiyaworanant, J. Roy. Inst. Thailand 2: 91 (2010).

Plants to 60 cm tall; basal leaf sheaths 2–5, alternate, margins not overlapping, open and up to half or apically free from pseudostem, apex shortly tapering, pale to light greyish green, paler or white at base, glabrous to shortly puberulous, whitish hirsute on margin. Petiole 5.5–12 cm long, upper ones longer, more or less narrowly channelled, wings not undulate. Ligule shortly puberulous, translucent to tinged with light faint brown. Leaves 3–7, weakly plicate, 13–32 × 4–10.5 cm, adaxially light to dark greyish green, sparsely whitish hirsute in 2 rows along secondary veins, very shortly hirsute on margin, abaxially light greyish to silvery green, glabrous. Basal inflorescence sheaths 2–5, alternate, overlapping but not fused, apex shortly tapering, light greyish green, basally paler, sparsely puberulous to puberulous. Inflorescence 4–51 cm long, light green, puberulous. Flowers spiral. Calyx
0.7–1.5 × 0.2–0.3 cm, divided up to 1/3 of calyx tube length, apex more or less acute to obtuse, light green, puberulous. Flora1 tube 1–1.7 cm long, light yellowish green to light green. 

Floral tube chamber 0.1–0.3 × 0.1–0.2 cm, light yellowish green to light green. Corolla dorsal lobe c.1.2 × 0.5 cm, lateral lobes c.0.9 × 0.2–0.3 cm, apex obtuse, light green almost translucent towards margin. Lateral staminodes obliquely obovate, reflexed with thickened upper margin, 0.5–0.6 × 0.2–0.3 cm, light yellowish green to green, darker at thickened margin, basal appendage protruding and ear-like, c.0.2 × 0.1 cm, glistening white. Labellum semilunar, c.0.7 × 0.5 cm, mid-region a channel leading into floral chamber, glistening white and becoming light yellowish green in chamber, side lobes flat, almost semicircular with recurved apical margin, light yellowish green to green, apex of 3 distinct projections: 2 vertical ones straight, like thick dorsal fins, glistening white, 1 horizontal one, straight, perpendicular to and between base of vertical pair, glistening white. Stamen: filament 0.6–0.9 cm, light yellowish green; anthers 0.3–0.5 cm, light yellowish green with whitish apex. Ovary 0.1–0.8 × 0.1–0.3 cm, light green, longitudinal grooves c.8, densely puberulous; nectaries c.0.2–0.3 × 0.05 cm long; style 2–3.4 cm long; stigma c.0.05 × 0.05 cm. Fruit more or less elongate, c.3–5 × 0.8–1.3 cm, light green to green, finely puberulous.

Etymology. Jules (or François-Jules) Harmand (1845–1921), French explorer in Indo-China. Hemiorchis thoreliana is named after Clovis Thorel (1833–1911), French explorer and botanist in Indo-China.
**Distribution.** Cambodia, Laos and Thailand (see Fig. 6). Perhaps also in Vietnam, if the type of *Hemiorchis thoreliana* really is from this country.

**Habitat and ecology.** 60–300 m altitude.

**Proposed IUCN status.** Least Concern (LC). AOO = 32 km², EOO = 187,651 km². This taxon appears to be less common than *Gagnepainia godefroyi*, but most of the collections have been made near or within protected areas.

**Specimens examined.** UNKNOWN LOCALITY. ix 1877, Harmand, F.J. s.n. (P, barcode no. P06136205). CAMBODIA. 1875, Godefroy-Lebeuf, A. s.n. (holo P, barcode no. P032686) – Type of *Hemiorchis harmandii* Baill. LAOS. ix 1877, Harmand, F.J. 5508 (P).

THAILAND. Chanthaburi: Pong Nam Ron, 21 iii 1971, Bogner, D.J. 1083 (K); Chonburi: Sriracha District, iv 1924, Collins, D.J. 1083 (K); ibid, 5 iv 1920, Marcant, A. 200 (BM); Khao Khieo, 7 iv 1975, Maxwell, J.F. 75-363 (BK); ibid, 17 iv 1976, Maxwell, J.F. 76-231 (BK). Mukdahan: Phu Mano, 13 v 1932, Kerr, A.F.G. 21434 (K). Saraburi: Khao Sam Lum, 27 iv 1974, Maxwell, J.F. 74-301 (BK); ibid, 1 vi 1974, Maxwell, J.F. 74-545 (BK).

VIETNAM (COCHINCHINE): 1862–1866, Thorel, C. s.n. (holo P) – Type of *Hemiorchis thoreliana* Baill. CULTIVATED AT RBGE. Originally from Thailand, Chachoengsao, Tha Takiap, Royal Forest Department Centennial Botanic Garden, RBGE living collection accession number 19991163A: 4 v 2001, Newman, M.F. 1202 (E); 8 v 2006, Newman, M.F. & Škorničková, J. 1468 (E); 2013 (exact date unrecorded) Tan, W.M.S. 6 (E); 25 iv 2013, *Tan, W.M.S.* 13 (E, flowers in spirit); 2013 (exact date unrecorded) *Tan, W.M.S.* 14 (E, fruit in spirit).

CULTIVATED AT SMITHSONIAN INSTITUTION. Originally from Thailand, living collection accession number USBRG 2001-114: 30 v 2002, Kress, W.J. & Bordelon, M.W. 02-7199 (US).

*Gagnepainia harmandii* is a distinct species with a more southerly distribution than *G. godefroyi*. Although *Gagnepainia harmandii* is similar in its vegetative morphology to *G. godefroyi*, there are vegetative characters that allow the two taxa to be distinguished from each other, as described above. *Gagnepainia harmandii* in bloom can hardly be confused with *G. godefroyi*, because it is characterised by flowers that are predominantly green and yellowish green, its labellum is half-moon–shaped with two flat side lobes that are almost semicircular with a recurved apical margin, the apex of the labellum is adorned with 3 distinct projections that are a glistening white colour, 2 vertical and 1 horizontal.

Only a single sheet of the type collection of *Hemiorchis harmandii* has been located during this study. Recognising that duplicates may yet be found in other herbaria, we designate this sheet at P, barcode P0032686, as the lectotype.

In 1895, when Baillon described *Hemiorchis godefroyi* and *H. harmandii* there was also a third species, *H. thoreliana*. Baillon was uncertain whether *Hemiorchis thoreliana* was a good species or merely a variety of *H. harmandii* but he proceeded to name it provisionally as a separate species.

Two specimens of *Hemiorchis thoreliana* have been found during this revision. One is Thorel s.n. (P032687) from Cochinchine, and the other is Harmand 1895 (P06136205) from an unknown collection locality. Thorel’s collection is labelled ‘*Hemiorchis*
thoreliana’ in Baillon’s handwriting and is marked as the type of this name, although it is impossible to be sure whether this was done in Baillon’s time. Harmand 1895 is labelled ‘Crescit in montibus Lakoon, 9/1877’. A second label, in Gagnepain’s handwriting states, ‘Confusion d’étiquettes. M. Pierre attribue à cette plante la localité du Gagnepainia godefroyi’, i.e. mixed labels. Mr Pierre attributes the locality of Gagnepainia godefroyi to this plant. Of these two collections, only Thorel’s was definitely seen by Baillon so we choose it here as the lectotype of Hemiorchis thoreliana.

Close examination of these specimens and comparison to Gagnepainia harmandii revealed no differences. Furthermore, an annotated illustration of a flower by Baillon attached to the holotype of Hemiorchis thoreliana clearly shows a flower bearing a labellum with two flat side lobes that are almost semicircular and, most significantly, the labellum apex is detailed with 3 (2 vertical : 1 horizontal) distinct projections. Considering all the available evidence, Hemiorchis thoreliana is placed in synonymy in this revision. There are no grounds to maintain it as a distinct species.

Baillon’s protologue (1895) is very unclear where the types of Gagnepainia harmandii and G. thoreliana were collected. Of the latter, he said nothing at all, and of the former he said simply that it was probably a Cambodian plant. The label of the type of Gagnepainia harmandii states in Baillon’s handwriting that it came from Cambodia. The label of the type of Gagnepainia thoreliana states only ‘Cochinchine’, which may refer to southern Vietnam but was also used until at least the 1940s to include Cambodia (see, for example, Gagnepain, 1944, p. 41, in which Godefroy is said to have accompanied Harmand ‘au Cambodge, en Cochinchine, où il récolta 882 échantillons reçus en 1876–8’). Thorel collected the type of Hemiorchis thoreliana during a long expedition along the River Mekong, which began in Saigon and passed through the Cambodian towns of Phnom Penh, Oudong, Siem Reap, Kratié and Stung Treng before crossing into Lao and Thai territories (Gagnepain, 1911). We have not been able to determine the collection localities of Thorel’s collection along this route, nor have we seen more recent collections of this species from Cambodia. In preparing Figure 6, we have placed the type of Gagnepainia harmandii in the centre of Cambodia and that of G. thoreliana in An Giang Province of Vietnam, very near the Cambodian border, because this is the best information we have. It should be noted, however, that no material of Gagnepainia has ever been seen by Trần Hữu Dang, one of the best Zingiberaceae collectors working in Vietnam (Trần Hữu Dang, Binh Duong, personal communication, June 2017).

2. Hemiorchis Kurz, J. Asiat. Soc. Bengal, Pt 2, Nat. Hist. 42: 108 (1873); Bentham, Gen. Pl. 3: 641 (1883); Petersen, Nat. Pflanzenfam. 2(6): 30 (1888); Baker, Curtis’s Bot. Mag. 116: t. 7120 (1890); Baker, Fl. Brit. India 6: 206 (1890); King, Ann. Roy. Bot. Gard. (Calcutta) 5: 163 (1894); Baillon, Bull. Mens. Soc. Linn. Paris 2: 1195 (1895); Gage, Rec. Bot. Surv. India 1(13): 362 (1901); Schumann, Pflanzenr. IV, 46 (Heft 20): 127 (1904); Mitra, Fl. Pl. E. India 1: 249 (1958); Rao & Verma, Bull. Bot. Surv. India 14(1–4): 119 (1972); Hara, Enum. Fl. Pl. Nepal 1: 61 (1978); Smith in Noltie, Fl. Bhutan 3(1): 198 (1994); Larsen, Fam. Gen. Vasc. Pl. 4: 488 (1998); Larsen & Triboun,
Deciduous and precocious understorey herbs to 85 cm tall, erect, individual plant of isolated pseudostems forming loose to dense spreading clumps. Rhizomes long, creeping and irregularly shaped, forming along the length of the rhizomatous roots, light brown. Rhizomatous roots creeping and fleshy, white when young, turning light brown with age. Feeder roots fine and numerous, white when young, turning light to dark brown with age. Pseudostems arising with plane of distichy of leaves parallel to rhizome, broad and almost flattened to rounded, with 2–6 basal leaf sheaths, pale to light green, with or without flush of maroon or light brownish pink, longitudinal venation distinct, puberulous, indumentum present along sheath margins. Petioles short to long with lamina decurrent, openly or narrowly channelled. Ligule perpendicularly encircling the inner circumference of the base of each petiole, very short and membranous, puberulous, almost translucent to tinged with a light reddish brown. Leaves 3–9 on each pseudostem, alternate, lanceolate, broadly lanceolate to slightly ovate, plicate, adaxially light to dark green, indumentum present along leaf venation, abaxially a contrasting light greyish to silvery green with or without flush of light maroon, puberulous or glabrous, base obtuse to rounded, apex acuminate or attenuate. Basal inflorescence sheaths 2–6, finely puberulous, pale to light green, with or without flush of maroon or pale to light reddish brown, with or without fine maroon specks, longitudinal venation distinct. Inflorescence a spike to 26.5 cm tall, erect, pale to light green or off-white to pale light brown, with or without fine maroon specks, darker at peduncle and lighter at rachis, finely puberulous. Floral bracts absent or, if present, curved, subulate, each subtending one flower. Flowers spirally arranged, sessile, zygomorphic, opening successively. Calyx infundibuliform, 3-lobed, divided up to 1/3 of calyx tube length, light green to light reddish brown with or without fine maroon specks on lobes, finely puberulous, persistent in fruit. Floral tube straight and slender, shorter than, or as long as to twice as long as calyx tube, off-white to light greenish yellow. Floral tube chamber cupuliform, dorsiventrally attached from base to floral tube, off-white to light pale yellow. Corolla lobes oblong to broadly oblong, dorsal lobe larger than or equal to lateral lobes, margins involute, pale to light creamy brown or light brownish pink, adaxially shortly puberulous, apex connate forming an acuminate tip. Lateral staminodes petaloid, paddle-shaped, obovate or shallowly concave, light creamy brown to brownish pink with or without pink or light yellow to orangey yellow, basal appendage flap-like, more or less triangular, light to dark brownish red or light to dark yellow with or without red markings. Labellum shallowly dish-like or deeply cymbiform, mid-region distinctly raised with a single broad keel or a double keel more or less channelled between, running the length of labellum from base to apex, with an appendage at base and a projection at apex, side lobes concave, adjoining both sides of labellum, variably coloured light yellowish brown, pinkish brown, maroon and yellow to orange. Stamen: short, slightly arching and glabrous,
filament short, shorter than or equal to anthers; anthers more or less rectangular with slightly recurved apex, thecae linear and exserted, pollen white to off-white. **Ovary** oblong to globose, light pale green to light yellowish brown, up to 10 longitudinal grooves present and densely puberulous, tricarpellate, unilocular, placentation parietal; epigynous nectaries 2, subulate; style filiform; stigma clavate to globose, exserted from apex of anther between thecae. **Fruit** a thick-walled capsule, more or less ellipsoid, with persistent calyx and remaining perianth shrivelled, light green to green or light creamy brown, with or without maroon specks, up to 10 longitudinal grooves and finely puberulous, dehiscing into three valves. **Seeds** obovoid to globose, attached to placentae by a short neck, light olive to brownish green and smooth. **Aril** translucent white, veil-like and only covering the neck or up to 1/3 of the seed.

**Distribution.** Three species ranging from eastern Nepal, southeastwards through north-eastern India (West Bengal, Meghalaya, Assam, Mizoram), Bangladesh, Burma and northern Thailand. We have not seen material which is definitely from Sikkim or Bhutan though parts of the south of Sikkim are at suitable altitude.

**Ecology.** Typically growing in partly shaded to shady understorey of bamboo, *Dipterocarpus* and mixed deciduous forest, and occasionally growing in association with limestone substrate.

*Hemiorchis* can be recognised by its orchid-like flowers, which are sessile with a densely puberulous ovary surmounted by an infundibuliform 3-lobed calyx, and a slender floral tube with a distinct, cupuliform floral chamber bearing the remaining orchid-like perianth. The three corolla lobes are generally flat with involute margins, and the petaloid staminodes are paddle-shaped, obovate or shallowly concave. The stout stamen comprises a short filament with rectangular anther, protruding from above the basal appendage of the labellum. The labellum is shallowly dish-like or deeply cymbiform and the mid-region distinctly raised with a single broad keel or a double keel more or less channelled between; this runs the length of the labellum from the base to the apex with an appendage at the base and a projection at the apex. The thick-walled capsules are usually formed by the basal flowers, occasionally by the apical ones. They are more or less ellipsoid with persistent calyx and are distinctly grooved and finely puberulous.

Determination of specimens from images is more difficult in *Hemiorchis* than in *Gagnepainia*. We cannot determine the specimens at CAL, which we have seen only as images. For this reason, we are not confident of the distributions of the species in India.

**Key to the species of Hemiorchis**

1a. Petiole > 4 cm, long, slender and narrowly channelled; leaves 3–6, elliptic to slightly ovate; staminodes with light to dark brownish red basal appendage; mid-region of labellum a single broad keel, apical projection a single to weakly bilobed or triangular to tridentate lobe ___________________________________________ 2.1. *H. burmanica*
1b. Petiole ≤ 4 cm, short, thick and openly channelled; leaves 5–9, lanceolate to broadly lanceolate; staminodes with light to dark yellow basal appendage, or without red markings; mid-region of labellum either a single broad or double keel, apical projection either a single blunt lobe or distinctly double keeled or bilobed _______________ 2

2a. Floral bracts absent or, if present, c.0.2–0.5 cm long, puberulous; apex of staminodes more or less truncate, light yellow to orangey yellow; labellum mid-region distinctly raised with a single broad keel, apical projection a single blunt lobe _______________ 2.2. H. pantlingii

2b. Floral bracts absent; apex of staminodes with weakly rounded uneven lobes, light creamy brown to brownish pink; labellum mid-region a double keel, more or less channelled, apical projection distinctly double keeled or bilobed _______________ 2.3. H. rhodorrhachis

2.1. Hemiorchis burmanica Kurz, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 42: 108 (1873); Bentham, Gen. Pl. 3: 641 (1883); King, Ann. Roy. Bot. Gard. (Calcutta) 5: 163 (1894); Schumann, Pflanzenr. IV, 46 (Heft 20): 127 (1904); Mitra, Fl. Pl. E. India 1: 250 (1958); Larsen & Triboun, Thai Forest Bull., Bot. 28: 39 (2000); Srivastava & Ghoshal, Bangladesh J. Pl. Taxon. 12(1): 59 (2005); Larsen & Larsen, Gingers of Thailand 103 (2006); Picheansoonthon, J. Roy. Inst. Thailand 1: 115 (2009); Singh, Indian J. Forest. 35(1): 97 (2012). – Type: Burma, Pegu Division, Karway (near Shwegyin), v 1868, W.S. Kurz 392 (lecto CAL, designated here).

Plants to 60 cm tall, pseudostems more or less rounded; basal leaf sheaths 4–6, alternate, margins not overlapping and open, apex shortly tapering, pale to light green, with or without flush of maroon, whitish hirsute on margin only to puberulous. Petiole 4–11.5 cm long, upper ones longer, slender and narrowly channelled. Ligule shortly puberulous, translucent to tinged with light reddish brown. Leaves 3–6, elliptic to slightly ovate, 6.5–23 × 4–8 cm, adaxially light green to green, whitish hirsute in 2 rows along secondary veins, denser along veins parallel to margin, abaxially light greyish to silvery green, glabrous or puberulous, base more or less obtuse to rounded or weakly, asymmetrically rounded, apex shortly acuminate to acuminate, margin entire. Basal inflorescence sheaths 2–5, alternate, margins overlapping but not fused, apex shortly tapering, pale to light green, with or without flush of maroon, basally paler, puberulous. Inflorescence 8–26.5 cm long, pale to light green, puberulous. Floral bracts absent or present. Calyx 0.7–1.2 × 0.2–0.4 cm, two lateral lobes larger, ventral lobe smaller or subequal, apex acute to shortly acuminate, pale to light green, with or without fine maroon specks at apex, puberulous. Floral tube 0.4–1 cm long, pale greenish yellow. Floral tube chamber 0.3 × 0.2–0.3 cm, light pale yellow. Corolla: dorsal lobe 1.2–2 × 0.7–0.9 cm, lateral lobes 1.1–1.5 × 0.4–0.5 cm, apex connate, shortly acuminate, margins involute, pale to light brownish pink, adaxial shortly puberulous, abaxial glabrous. Lateral staminodes paddle-shaped, apex weakly sinuate, 1–1.2 × 0.5–0.6 cm, light brownish pink or light yellow to orangey yellow, with or without a darker band at the apex, basal appendage flap-like, more or less triangular, c.0.1 cm, light to dark brownish red. Labellum deeply cymbiform, 1–1.2 × 1–1.2 cm, mid-region distinctly raised with a single broad keel, largely yellow to orangey yellow and brownish red towards the base, basal appendage flap-like, more or less bilobed,
c.0.1 × 0.1 cm, light to dark brownish red, apical projection a single to weakly bilobed or triangular to tridentate lobe, yellow to orangey yellow, side lobes light brownish pink or light yellow to orange with maroon specks, dark brownish red towards and along basal portion of keel, with or without a band of yellow or pink at the apex. **Stamen**: filament 0.4 cm long, light pale yellow; anthers 0.4 cm long, light pale yellow, with or without fine maroon specks at apex. **Ovary** 0.1–0.4 × 0.1 cm, pale to light green, c.10 longitudinal grooves present and densely puberulous; nectaries c.0.3 × 0.05 cm long; style c.1.5 cm long; stigma c.0.1 × 0.05 cm. **Fruit** more or less ellipsoid, c.0.7–1.5 × 0.4–1 cm, light green to green, finely puberulous.

**Etymology.** Latin, from Burma.

**Distribution.** Burma and Thailand (Fig. 8).
Habitat and ecology. 550–1100 m altitude.

Proposed IUCN status. Least Concern (LC). AOO = 48 km², EOO = 265,731 km². Collections of this taxon occur mostly near or within protected areas across its range, and apart from the type collection, more recent collections have also been made.

Specimens examined. Burma. Burma, Magway, Minbu District, acc. no. 1 vouchered as 22 v 2002, Kress, W.J. & Brothers, L. 02-7193 (US); ibid, 26 vi 1999, Kress, W.J. et al. 99-6453 (US); Burma, Mandalay Division, Maymyo, Maymyo, 7 vi 2001, Kress, W.J. et al. 01-6879 (US); Burma, Mandalay Division, Thabeikkyin Township, 11 vi 2001, Kress, W.J. et al. 01-6889 (US); ibid, 9 vi 2001, Kress, W.J. et al. 01-6884 (US); Burma, Pegu Division, Padaung Township, 22 iv 2000, Kress, W.J. et al. 00-6677 (US); Burma, Pegu Division, Shwegyin, 18 v 1868, Kurz, W.S. 392 (lecto CAL) – Type of Hemiorchis burmanica Kurz; Burma, Pegu Division, Sittang River, Kurz, W.S. s.n. (syn K) – Type of Hemiorchis burmanica Kurz; Burma, Pegu Division, Yènwè Chaung, 4 v 1871, Kurz, W.S. 3299 (syn K) – Type of Hemiorchis burmanica Kurz.

CULTIVATED AT RBGE. Originally from Thailand, Tak, Mae Ramat, RBGE living collection accession number 19871260A: 20 v 1999, Newman, M.F. 861 (E); 19 vi 2013, Tan, W.M.S. 8 (E); 15 vi 2013, Tan, W.M.S. 12 (E).

Kurz’s original material, as cited in the protologue, consists of plate 8, which is a line drawing, and reference to three localities, namely, Pegu, Martaban and Tenasserim. We have found four collections of this species made by Kurz that are original material.

1. Kurz 3299 (K, barcode K000640568), collected on 4 May 1871 at Theywa on the Ye Nwe stream (Ye noë choung) in Pegu.
2. Kurz s.n. (K, barcode K000640567), without date, collected in the Sittang Valley, labelled ‘raised from roots brought home by me’.
3. Kurz 329 (CAL, barcode CAL0000026424), collected in Martaban at an unknown date.
4. Kurz 329 (CAL, without barcode), collected at ‘Karway, Low forest’ in Pegu. We cannot locate Karway but Kurz mentions reaching this place on 18 May 1868, after leaving Shwegyin. This specimen closely resembles plate 8 of the protologue and is evidently the one from which the plate was drawn.

The number ‘329’ on the specimens at CAL may be a species number rather than a collection number, because these are clearly not part of a single gathering. The specimen collected at Karway is chosen as lectotype because it is so obviously the one on which the plate in the protologue was based.

2.2. Hemiorchis pantlingii King, Ann. Roy. Bot. Gard. (Calcutta) 5(2): 163 (1896); Schumann, Pflanzenr. IV, 46 (Heft 20): 127 (1904); Mitra, Fl. Pl. E. India 1: 250 (1958); Rao & Verma, Bull. Bot. Surv. India 14(1–4): 119 (1972); Hara, Enum. Fl. Pl. Nepal 1: 61 (1978); Smith in Noltie, Fl. Bhutan 3(1): 198 (1994); Lucksom, J. Bombay Nat. Hist. Soc. 98(3): 493 (2001). – Type: India, West Bengal, Darjeeling, Mungpoo (Mongpu), 300–1060 m, 1891, R. Pantling (lecto K [K000640570], designated here; isolecto BM [BM000958129], K [K000640571], P [P00686501]).
Plants to 85 cm tall, pseudostems broad and more or less flattened; basal leaf sheaths 3–5, alternate, not overlapping and open, apex shortly tapering, pale to light green, basal ones puberulous, upper one whitish hirsute on margin only. *Petiole* c.3.5 cm long. *Ligule* puberulous. *Leaves* 5–8, lanceolate to broadly lanceolate, 19–36 × 5–9 cm, adaxially darker green, whitish hirsute in 2 rows along secondary veins, denser along veins parallel to the margin, abaxially light greyish green, largely glabrous, appressed hirsute only on veins parallel to margin and apical region of primary vein, base attenuate to more or less obtuse, apex attenuate, margin entire. *Basal inflorescence sheaths* 3–6, alternate, overlapping but not fused, apex shortly tapering, pale to light green, basally paler, puberulous. *Inflorescence* 9–18 cm long, pale to light green, puberulous. *Floral bracts* absent or, if present, c.0.2–0.5 cm long, puberulous. *Calyx* c.0.4–0.7 × 0.3–0.5 cm, lobes equal to subequal, apex acute, pale to light creamy brown, puberulous. *Floral tube* c.0.5–0.9 cm long. *Floral tube chamber* c.0.2–0.3 × 0.1–0.2 cm. *Corolla*: dorsal lobe c.1–1.2 × 0.5–0.8 cm, lateral lobes c.0.8–0.9 × 0.4 cm, apex conuate, shortly acuminate, margins involute, pale to light creamy brown, adaxial shortly puberulous, abaxial glabrous. *Lateral staminodes* obovate, apex more or less truncate, c.0.9 × 0.6 cm, light yellow to orangey yellow, with or without a darker band at apex, basal appendage flap-like, more or less triangular, c.0.1 cm, light to dark yellow, with or without red markings. *Labellum* deeply cymbiform, c.0.9–1 × 1 cm, mid-region distinctly raised with a single broad keel, largely yellow to orangey yellow and brownish red towards base, basal appendage flap-like, more or less bilobed, c.0.1 × 0.15 cm, light to dark yellow, with or without red markings, apical projection a single blunt lobe, yellow to orangey yellow, side lobes light yellow to yellowish orange, dark brownish red towards and along basal portion of keel, with a band of yellow or yellowish orange at apex. *Stamen*: filament c.0.3 cm long, light pale cream; anthers c.0.3 cm long, light pale cream. *Ovary* c.0.2–0.3 × 0.1–0.15 cm, pale to light creamy brown, c.6 longitudinal grooves present and densely puberulous; nectaries not seen; style c.1.6 cm long; stigma c.0.05 × 0.05 cm. *Fruit* not seen.

*Etymology*. Robert Pantling, 1856–1910, British plant collector.

*Distribution*. India, Nepal (see Fig. 8).

*Habitat and ecology*. Between 300 and 1210 m altitude.

*Proposed IUCN status*. Data Deficient (DD). AOO = 20 km², EOO = 2655 km². This taxon has been collected only five times, most recently in 1971. Potential or real threats, other than general disturbance of natural habitats by people, are unknown.

*Specimens examined*. **INDIA**. West Bengal, Darjeeling District, Chunābāti, iv 1876, Gamble, J.S. 617A (K); Sivok, iii 1873, Gamble, J.S. 4015B (K); Sikkim Himalaya, 1000–4000 ft, 1893, Pantling, R. s.n. (BM, E, K [2 sheets], P, U, US, syn of *Hemiorchis pantlingii* King); Mungpoo, 1000–3500 ft, 1891, Pantling, R. s.n. (K, lecto of *Hemiorchis pantlingii* King; isolecto BM, K, P).

**NEPAL**. Nepal, Soktim Tea Estate, Mai Khola, 19 iv 1971, Stainton, J.D.A. 6795 (BM).
King’s protologue cites the following material: “Sikkim Himalaya; growing in sand by the sides of streams from 800 to 3,500 feet. R. Pantling.” Two collections, each represented at a number of herbaria, correspond closely but not exactly to this citation. Pantling s.n., collected at 1000–3500 ft at Mungpoo (modern Mongpu) in 1891 is present at BM, K (2 sheets) and R. Pantling s.n., collected at 1000–4000 ft at an unrecorded locality in Sikkim Himalaya in 1893 is present at BM, E, K (2 sheets), P, U and US. Although Pantling’s collections are all labelled ‘Sikkim Himalaya’, it is not clear whether any of them came from what is now the state of Sikkim.

2.3. Hemiorchis rhodorrhachis K.Schum., Pflanzenr. IV, 46 (Heft 20): 128 (1904); Mitra, Fl. Pl. E. India 1: 250 (1958); Rao & Verma, Bull. Bot. Surv. India 14(1–4): 119 (1972); Srivastava & Ghoshal, Bangladesh J. Pl. Taxon. 12(1): 59 (2005); Larsen & Larsen, Gingers of Thailand 104 (2006). – Type: Cultivated at Royal Botanic Gardens, Kew, 20 iii 1889, annotated “Type specimen of Bot. Mag. t. 7120”, (lecto K, designated here [K000640564]). Presumably grown from G. Mann’s collection in India, Meghalaya, Khasi Hills, Terriaghat. Figs 3C, 9.

Hemiorchis burmanica auctt. non Kurz: Baker, Curtis’s Bot. Mag. 116: t. 7120 (1890), Fl. Brit. India 6: 207 (1890); Gage, Rec. Bot. Surv. India 1(13): 362 (1901).

Plants to 45 cm tall, pseudostems broad and more or less flattened; basal leaf sheaths 2–4, alternate, margins not overlapping and open, apex shortly tapering, pale to light green or light brownish pink, whitish hirsute on veins parallel to margin or on margin only. Petiole 1–4 cm long, upper ones longer, broadly channelled. Ligule shortly puberulous, translucent to tinged with faint brown. Leaves 5–9, lanceolate, 9–25 × 3–7.5 cm, adaxially light green to green, whitish hirsute in 2 rows along secondary veins, denser along veins parallel to the margin, abaxially light greyish green, largely glabrous, sometimes with appressed hairs on veins parallel to margin and at apical region of primary vein, base attenuate to more or less obtuse, apex attenuate, margin entire. Basal inflorescence sheaths 3–6, alternate, overlapping but not fused, apex shortly tapering, pale to light green or pale to light reddish brown, with or without fine maroon specks, basally paler, puberulous. Inflorescence 7–22 cm long, pale to light green or off-white to pale light brown, with or without fine maroon specks, basally paler, puberulous. Floral bracts absent. Calyx c.0.5–1 × 0.3–0.6 cm, lobes equal to subequal, apex acute or shortly acuminate, pale to light green or pale to light reddish brown, with or without fine maroon specks, basally paler, puberulous. Floral tube c.0.5–1.5 cm long, off-white. Floral tube chamber 0.2–0.4 × 0.2–0.3 cm, off-white. Corolla: dorsal lobe 1–2.2 × 0.4–0.9 cm, lateral lobes 0.8–1.8 × 0.4–0.7 cm, apex connate, shortly acuminate, margins involute, pale to light brownish pink, adaxially shortly puberulous, abaxially glabrous. Lateral staminodes obovate, apex with weakly rounded, uneven lobes, c.0.8–1.5 × 0.6–1 cm, light creamy brown to brownish pink, with or without a darker band at apex, basal appendage flap-like, more or less triangular, c.0.1 cm, light to dark yellow, with or without red markings. Labellum deeply cymbiform, 1–1.5 × 1.2–1.8 cm, mid-region a double keel, more or less channelled, largely yellow to orangey yellow and brownish red towards base, basal appendage flap-like, more or less bilobed, c.0.1 × 0.2 cm, light to dark
yellow, with or without red markings, apical projection distinctly double keeled or bilobed, yellow to orangey yellow, side lobes light creamy brown or yellow, dark brownish red or red towards and along basal portion of keel, with a band of yellow to yellowish orange or brownish pink at apex. Stamen: filament 0.3–0.4 cm long, white to light pale cream; anther c.0.3–0.5 cm long, white to light pale cream. Ovary c.0.1–0.4 × 0.1–0.2 cm, pale to light green or creamy brown, c.10 longitudinal grooves present and densely puberulous; nectaries c.0.3 × 0.05 cm long; style 1.3–2.7 cm long; stigma c.0.07 × 0.05 cm. Fruit elliptic, c.1.1–3 × 0.6–1 cm, pale to light green or creamy brown, with or without maroon specks, finely puberulous.

Etymology. Greek, red rachis.
Distribution. India, Bangladesh, Burma, Thailand (see Fig. 8).

Habitat and ecology. From 10 to 910 m altitude.

Proposed IUCN status. Least Concern (LC). AOO = 44 km², EOO = 421,511 km². Some collections of this taxon occur near or within protected areas across its range, and apart from the type collection, recent collections have also been made as seen in the specimens studied.

Specimens examined. Bangladesh. Chittagong, Chittagong Hill Tracts District, iii 1938, Wenger, W.J.L. 532 (K); Cox’s Bazar District, Baniar Chara Dipterocarp Forest, 10 ix 1999, Newman, M.F. & Rahman, M.A. 1001 (E).

India. Meghalaya, Khasi Hills, 1886, Mann, G. s.n. (K).

Thailand. Mae Hong Son, Doi Tham Makaeng, 22 v 1921, Kerr, A.F.G. s.n. (BM, BM0011115157); Tak, Mae Sot, environs of Ban Phu Pae, 27 v 1979, Vidal, J.E. et al. 6070 (P, P01743362); ibid, 28 v 1979, Vidal, J.E. et al. 6114 (P, P01743361).

Cultivated at RBGE. Originally from Bangladesh, Chittagong, Cox’s Bazar District, Baniar Chara Dipterocarp Forest, RBGE living collection accession number 19991652A: 13 iv 2011, Newman, M.F. 2452 (E); ibid, 19 vii 2013, Tan, W.M.S. 7, 10 & 11 (E).

Cultivated at RBG Kew. Originally from India, exact locality unknown, Lobb, T. s.n. (K); Meghalaya, Khasi Hills, Terriaghat, 1 ix 1888, Mann, G. s.n. (K K000640565); ibid, iii 1888, Mann, G. s.n. (K, K000640566); 20 iii 1889; ibid, Anon s.n. (K, K000640564, lecto of Hemiorchis rhodorrhachis).

Cultivated at NMNH Botany Research Greenhouses, USA. Originally from Burma, Magwe Division, 9 vi 2010, Kress, W.J. & Bordelon, M.W. 10-8756 (US); Sagaing Division, Kalewa Township, 18 vi 2001, Kress, W.J. et al. 01-6925 (US, 00605447); Kani Township, Alaungdaw Kathapa National Park, 5 miles north of Shrine, along Min Dan Chuang, 15 iv 2000, Kress, W.J. et al. 00-6666 (US, 2 sheets, 00605070 & 00605071); ibid, 28 v 2002, Kress, W.J. & Bordelon, M.W. 02-7195 (US, 00732639).

In the protologue, Schumann (1904: 128) cited a single collection as follows, “In den Khasia-Bergen, lebend eingesandt nach Kew von Gustav Mann, blühte dort.” Additionally, he referred to Hemiorchis burmanica sensu Baker in Curtis’s Botanical Magazine (1890: t. 7120) and in the Flora of British India (1890: 207). The original material of Hemiorchis rhodorrhachis thus comprises a herbarium collection made from a plant cultivated at Kew and a painting in Curtis’s Bot. Mag. Three sheets were found in a type cover at K, Anon s.n. (K000640564), Mann, G. s.n. (K000640565) and Mann, G. s.n. (K000640566). Each was collected on a different date, so they are not parts of a single gathering. The sheet with barcode K000640564 bears an annotation reading, “Type specimen of Bot. Mag. t. 7120”. We regard this and the painting in Curtis’s Bot. Mag. as original material. Of the specimen and the painting, we select the specimen as the lectotype of Hemiorchis rhodorrhachis. It is uncertain whether specimens K000640565 and K000640566 are part of the original material. If they are, they are syntypes, not isolecotypes.
**Uncertain Species**

W.J. Kress 99-6515 (US) is a specimen made from living accession USNM 98-196 in the Research Greenhouses of the Smithsonian Institution. The living material was originally collected in July 1998 at Ban Pang Mu, Mae Hong Son Province, Thailand, by W.J. Kress, M.W. Bordelon & M. Collins with field number 98-6242. The living plant died while dormant in 2003–2004. Photographs on the website of the Smithsonian Institution (Smithsonian Institution, no date) show characters of the labellum and lateral staminodes that do not match those of *Hemiorchis burmanica*. This collection may represent a new taxon but cannot be studied further until it is collected again.

**Excluded Name**

*Hemiorchis habessenica* Ehrenb. ex Schweinf., Beitr. Fl. Aethiop. 241 (1867), was cited as an unpublished synonym of *Lindenbergia scutellarioides* Asch. (Orobanchaceae), so it is an invalid name (Turland *et al.*, 2018; Art. 36.1(c)).

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In the following index, accepted taxa are given in roman font and synonyms in italic. The number after each name refers to the taxon in the text above.

**Gagnepainia K.Schum.** (1)

Gagnepainia godefroyi (Baill.) K.Schum. (1.1)

Gagnepainia harmandii (Baill.) K.Schum. (1.2)

**Gagnepainia thoreliana** (Baill.) K.Schum. (1.2)

**Hemiorchis Kurz** (2)

Hemiorchis burmanica Kurz (2.1)

**Hemiorchis godefroyi** Baill. (1.1)

**Hemiorchis harmandii** Baill. (1.2)

Hemiorchis pantlingii King (2.2)

Hemiorchis rhodorrhachis K.Schum. (2.3)

**Hemiorchis thoreliana** Baill. (1.2)

### Appendix

**Appendix Table 1.** Primers used in the present study

| Region | Primer | Sequence | Reference |
|--------|--------|----------|-----------|
| ITS    | P17    | 5′-CTACCGATTGAA TGGTCCGGTGA-3′ | Popp & Oxelman (2001) |
| ITS    | 26S-82R | 5′-TCCCCGTTCGCTC GCCGTTACTA-3′ | Popp & Oxelman (2001) |
| matK   | mIF    | 5′-GTTCAGTACTTGTG AAACGTT-3′ | Kress et al. (2002) |
| matK   | m8R    | 5′-CTTCGACTTTTC TTGTGCT-3′ | Kress et al. (2002) |
### Appendix Table 2. PCR recipe for both regions (internal transcribed spacer and *matK*)

| Component                        | Volume  |
|----------------------------------|---------|
| dNTPs (2 mM)                     | 1 μL    |
| 10 × NH₄ reaction buffer         | 2.5 μL  |
| MgCl₂ (50 mM)                    | 1.5 μL  |
| F primer (10 μM)                 | 1.25 μL |
| R primer (10 μM)                 | 1.25 μL |
| Bovine serum albumin (1 μg/μL)   | 0.125 μL|
| Taq (5 U/μL)                     | 0.125 μL|
| Template                         | 1 μL    |
| Double-distilled H₂O             | 16.25 μL|
| Total volume                     | 25 μL   |

### Appendix Table 3. PCR profile for the internal transcribed spacer region

| Temperature | Duration |
|-------------|----------|
| 95°C        | 5 min    |
| 95°C        | 30 s     |
| 58°C        | 1 min    |
| 72°C        | 1 min    |
| 72°C        | 5 min    |
| 10°C        | Forever  |

\[ \times 35 \text{ cycles} \]

### Appendix Table 4. PCR profile used for the *matK* region

| Temperature | Duration |
|-------------|----------|
| 95°C        | 5 min    |
| 95°C        | 45 s     |
| 55°C        | 30 s     |
| 72°C        | 1 min    |
| 72°C        | 10 min   |
| 10°C        | Forever  |

\[ \times 35 \text{ cycles} \]