A revision of *Rhapis* (Arecaceae)

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Abstract

A revision of the Asian palm genus *Rhapis* is given based on study of 167 herbarium specimens of wild origin from A, AAU, BH, BK, BKF, GH, HN, HNU, HPNP, IBSC, K, KUN, L, MO, NY, P, SYS, US and application of the Phylogenetic Species Concept to a database comprising 13 qualitative and 16 quantitative variables. Eleven species are recognized, including two new ones. Two species are divided into subspecies.

Keywords: dioecy, Palmae, Vietnam, China

Introduction

*Rhapis* is the name given to small, clustering, fan-leaved, dioecious palms that can form large colonies by rhizomes in the understory of tropical and subtropical Asian forests, often on limestone soils. The species are distributed from southern China through Vietnam, Laos, Thailand, and Cambodia, with an outlying population in western Sumatra. The first revision of the genus was that of Beccari (1931), where five species were recognized. Bailey (1939) recognized nine species, and in the most recent revision, Hastings (2003) recognized eight species.

Despite this relatively recent revision, there are still taxonomic problems in *Rhapis*. Firstly, there are problems with cultivated plants. Some species of *Rhapis* are easily and commonly cultivated, and the introduction of plants from China into Japan took place in the seventeenth century (Bailey 1939, Yamaguchi & Barry 1974). Since then, *Rhapis* species, particularly *R. excelsa* and *R. humilis*, have been cultivated throughout tropical and subtropical areas of the world, and also as indoor plants. This long period of cultivation has produced numerous cultivars, and also some confusion over the naming of the cultivated species. Except for a few types, specimens from cultivated plants have been mostly ignored in the present study. This is because the numerous cultivars confuse species boundaries, and species have been introduced into areas where they are not native, confusing geographic boundaries.

Second, Hastings (2003) examined a limited number of specimens of wild origin, approximately 35. In the current revision 167 specimens of wild origin have been examined, representing 11 species. The biggest difference between the two revisions is Vietnam; Hastings cited four specimens from Vietnam representing three species; in the current revision 73 specimens from Vietnam have been examined, representing seven species. Vietnam is the center of diversity of the genus.

Third, Hastings used character states that are here considered difficult to distinguish, particularly leaf sheath fibers. Segment splitting has also been found problematic. In general, characters are difficult to define and score in *Rhapis*, making species difficult to delimit. Floral morphology can change quite dramatically during development, such that flowers of the same species from different stages of development appear different. This has led to misidentifications. New characters have therefore been sought in this study, and most of the qualitative variables used here have not been used before in *Rhapis*.

For all these reasons a new revision is presented here, based on the strict application of an explicit methodology, as explained below.
Materials and Methods

In this study, the Phylogenetic Species Concept (PSC) is used. Under the PSC, species are defined as: “the smallest aggregation of populations... diagnosable by a unique combination of character states in comparable individuals” (Nixon & Wheeler, 1990). Characters are qualitative variables that are consistent in all comparable individuals within a terminal lineage (i.e., species), and traits are qualitative variables with more than one state within species (i.e., polymorphic).

According to Davis and Nixon (1992), phylogenetic species are delimited by successive rounds of aggregation of local populations (population aggregation analysis—PAA), based on analysis of characters and traits. However, herbarium specimens are seldom collected on a population basis, and because there is no a priori method of placing specimens in populations and consequently distinguishing a priori between characters and traits, this kind of analysis is problematic. Nevertheless, specimens still need to be identified to species before the analysis can begin. Other methods, such as those used by Henderson (2011) are based on circular reasoning and lead to the elimination of traits for the whole genus, but clearly some qualitative variables could function as traits in some species and characters in others. In this study, a new methodology is used to apply the PSC, as follows.

The first stage was to determine to species all specimens examined according to either determinations on the specimens themselves or using the key in Hastings (2003). This stage led to recognition of what are here termed ‘preliminary species’. The next stage was to score, for all specimens, quantitative and qualitative variables (Appendix 1). At the same time as quantitative variables were scored, location (latitude, longitude, elevation) and quantitative variables were also scored, when possible. Completion of this stage led to a matrix of specimens determined to preliminary species and scored for location, quantitative, and qualitative variables (http://sciweb.nybg.org/Science2/res/Henderson/Rhapis.xlsx.zip).

The third stage was to examine, species by species, the states of each qualitative variable. There were two possible outcomes of this examination. Either the states of all qualitative variables were consistent within a preliminary species, or one or more qualitative variable varied within a preliminary species. Polymorphic preliminary species were ‘split’ so that they became two (or more) taxa with consistent qualitative variables. These taxa were then tested to look for corroborating evidence that they are separate taxa, i.e., whether the two were geographically separate, or whether there were quantitative differences between the two. If no such evidence was found, then the polymorphic preliminary species were treated as phylogenetic species with polymorphic characters treated as traits.

The next stage was to compare preliminary species with one another. If two or more preliminary species had the same combination of character states then they were combined into one phylogenetic species. If a preliminary species had unique combinations of character states it was treated as a phylogenetic species. Finally, geographic distributions of all accepted species were examined to look for evidence of disjunction. If two or more geographically separate populations were found, quantitative variables were tested to look for evidence of subspecific populations.

The result of these five stages were that preliminary species were tested as hypotheses and either supported or not; and new hypotheses of characters and traits (i.e., phylogenetic species) were presented and are used in the treatment.

The genus description given here is a summary of the qualitative and quantitative variables given in Appendix 1. Other descriptions are given in Hastings (2003) and Dransfield et al. (2008). Herbarium abbreviations are from Thiers (continuously updated).

The key is designed to show presumed relationships, although there is no phylogeny as yet for the genus. There appear to be three groups of species. Rhapis laosensis differs from all other species in its inflorescence morphology. Rhapis excelsa, R. subtilis, and R. kebangensis appear similar to one another based on their glabrous rachillae, corollas with internally swollen apical lobes and fruits borne on a persistent, swollen perianth. The seven other species (R. micrantha, R. humilis, R. robusta, R. gracilis, R. evansii, R. puhuongensis, and R. vidali) appear similar in morphology based on their tomentose rachillae, corollas with poorly developed apical lobes that are not swollen internally, and fruits borne on a pedicelliform pistillate corolla. Amongst these, R. evansii, R. puhuongensis, and R. vidali are similar in their pedicellate flowers.

Results

Application of the PSC to the database comprising 13 qualitative and 16 quantitative variables resulted in the recognition of 11 species. Examination of geographic distributions of these species led to recognition of subspecies in two species.
Key to the species of *Rhapis*

1. Prophyll and peduncular bract broad, flattened, completely overlapping, the inflorescences exerted laterally through the bracts on a recurved peduncle; Central Laos, eastern Thailand, central Vietnam ................................................................. *R. laosensis*  
   - Prophyll and peduncular bract narrow, tubular, not or scarcely overlapping, the inflorescences exerted apically through the bracts on a recurved peduncle .................................................................................................................. 2

2. Rachillae not filiform, glabrous; staminate and pistillate corollas with poorly developed, inturned apical lobes, these swollen internally; fruits borne on a pedicelliform pistillate corolla; China (Guangxi, Hainan, Hong Kong), northern and central Vietnam ............................................................. *R. excelsa*  
   - Central segments lanceolate or elliptic, acuminatus, the apices oblique, toothed; abaxial surface of segments without scales ........................................ 4

3. Central segments linear-lanceolate, not acuminate, the apices truncate, toothed; abaxial surface of segments with minute, brown scales; southern China (Guangdong, Hainan, Hong Kong), northern and central Vietnam ......................................................................................................................... *R. kebangensis*  
   - Abaxial surface of segments not indumentose when first exposed; Central Laos, south-central and Peninsular Thailand, western Cambodia, and western Sumatra ................................................................. *R. subtilis*  

5. Staminate and pistillate flowers pedicellate ................................................................. 6  
   - Staminate and pistillate flowers sessile ............................................................................ 8

6. Central segments elliptic, multi-veined, acuminate, the apices oblique, toothed, 3.1(1.8–4.2) cm wide; central Laos .......... *R. evansii*  
   - Central segments narrowly linear, usually 1–2-veined, acuminate, the apices scarcely toothed, 0.6(0.4–1.2) cm wide ................... 7

7. Segments 7(5–9) per leaf; central segments free almost to the base; northern Vietnam (Hoa Binh, Thanh Hoa) ............ *R. vitalii*  
   - Segments 15(15–16) per leaf; central segments joined at the base; Vietnam (Nghê An) .............................................................. *R. puhuongensis*  
   - Rachillae filiform, usually tomentose, especially the staminate ones; staminate and pistillate corollas with poorly developed, inturned apical lobes, these not swollen internally; fruits borne on a pedicelliform pistillate corolla ........................................... 5

8. Segments 18(13–28) per leaf; central segments linear-lanceolate, usually 1–2-veined, the apices scarcely toothed; China (Guangxi, Guizhou, Yunnan) ......................................................................................................................... *R. humilis*  
   - Segments 5(2–13) per leaf; central segments lanceolate or elliptic, usually multi-veined, the apices oblique, toothed ............... 9

9. Ligules scarcely developed; abaxial surface of segments with minute, brown scales; China (Guangxi, Guangdong, Hainan) .......... *R. gracilis*  
   - Ligules acute, solid, more or less persistent, or ligules acute, soon disintegrating; abaxial surface of segments without scales .... 10

10. Ligules acute, soon disintegrating; central segments free almost to the base, rarely joined at the base, the non-split basal part 0.7(0.1–2.5) cm; northern Vietnam (Ninh Binh, Thanh Hoa) .................. *R. micrantha*  
   - Ligules acute, solid, more or less persistent; central segments joined at the base, the non-split, basal part 3.3(1.4–5.3) cm long; northern Vietnam (Cao Bang, Ha Giang) and adjacent China (Guangxi) ........................................................................................................ *R. robusta*
FIGURE 1. Type specimen of *Rhapis evansii*.
1. *Rhapis evansii* Henderson sp. nov. Type:—LAOS. Vientiane: Vangvieng district, Ban Nathong, Tham Poukham, 18° 55′N, 102° 24′ E, 250–350 m, 1 August 1999, *T. Evans* 56 (holotype K!, barcode K000462531). (Fig. 1)

*Rhapis evansii* differs from all other species except *R. puhuongensis* and *R. vidalii* by its pedicellate flowers; it differs from both of these in its elliptic, multi-veined, acuminate central segments with the apices oblique and toothed.

**Stems** 0.8 m long, 0.5 cm diameter. **Leaf** sheath fibers coarse, flattened, forming a diagonal mesh, extended into a well-developed ligule; petioles 15.0 cm long, 1.1 mm wide at the apex; abaxial hastula usually complete, a low ridge separating petiole apex from costa; segments 6 per leaf; central segments elliptic, multi-veined, acuminate, the apices oblique, toothed, 23.0 cm long, 2.7 cm wide at midpoint, free almost to the base, the non-split part 0.2 cm; lateral segments 21.0 cm long, 1.0 cm wide at midpoint, the non-split basal part 0.3 cm; abaxial surface of segments without scales, not indumentose when first exposed. **Inflorescences** slender; prophyll and peduncular bract narrow, tubular, not or scarcely overlapping, the inflorescences exerted apically through the bracts on a curved peduncle; rachis length not recorded; rachillae slender, filiform, usually <1 mm wide; rachillae length not recorded; flowers pedicellate; flowers and fruits not recorded.

![Distribution maps](image-url)

**FIGURE 2.** Distribution maps of *Rhapis evansii*, *R. excelsa*, *R. gracilis*, and *R. humilis*. 

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**A REVISION OF RHAPIS**

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Distribution and habitat:—Central Laos in lowland forest on karst limestone outcrops at 250–350 m elevation (Fig. 2).

Taxonomic notes:—Although complete inflorescences and flowers are not known, the species is immediately distinguished by the combination of elliptic segments and pedicellate flowers.


*Rhapis flabelliformis* L’Héritier de Brutelle ex Aiton (1789: 473). Type:—Cultivated plant in J. Gordon’s garden, no date, no collector (holotype BM n.v., BM image!).

*Rhapis major* Blume (1836: 55). Type:—No locality, no date, *C. Blume s.n.* (holotype L n.v.).

*Rhapis javanica* Blume (1836: 56). Type:—INDONESIA. Java. No locality, no date, *C. Blume s.n.* (holotype L!).


Stems 2.3(0.5–4.0) m long, 0.9(0.4–1.4) cm diameter. Leaf ligules acute, soon disintegrating; petioles 29.5(5.7–63.0) cm long, 3.0(1.4–4.6) mm wide at the apex; abaxial hastula usually complete, a low ridge separating petiole apex from costa; segments 8(2–12) per leaf; central segments linear-lanceolate, usually multi-veined, not acuminate, the apices truncate, toothed, 27.6(13.7–39.5) cm long, 3.5(1.7–7.2) cm wide at midpoint, joined at the base, the non-split basal part 4.3(0.8–9.8) cm; lateral segments 24.3(14.0–35.0) cm long, 2.4(1.0–3.8) cm wide at midpoint, the non-split basal part 2.4(0.7–4.7) cm; abaxial surface of segments with minute, brown scales, not indumentose when first exposed.

Inflorescences small to large, with the first branch almost as large as the rest of the inflorescence; propyll and peduncular bract narrow, tubular, not or scarcely overlapping, the inflorescences exerted apically through the bracts on a curved peduncle; rachis 16.9(7.2–24.5) cm long; rachillae not filiform, glabrous; proximal rachilla 9.7(5.7–14.5) cm long, 1.1(0.8–1.6) mm wide; staminate and pistillate flowers sessile; staminate and pistillate corollas with well developed, erect, triangular apical lobes, these swollen internally; filaments keeled; fruits globose, color not recorded, 8.5(7.6–9.3) mm long, 7.0(6.1–7.7) mm diameter, borne on a swollen, persistent perianth.

Distribution and habitat:—Southern China (Guangdong, Hainan, Hong Kong) and northern and central Vietnam (Fig. 2) in lowland rain forest at 211(5–800) m elevation.

Taxonomic notes:—Hastings (2003) designated a Thunberg specimen (*sheet number 24386* at UPS), consisting of a single leaf, as lectotype of *Rhapis excelsa*. However, she then designated the same sheet as lectotype of *Rhapis flabelliformis*. This is superseded here. *Rhapis flabelliformis* is considered a synonym of *R. excelsa*, and although the plate by L’Héritier de Brutelle originally cited by Aiton (1789) has not been found (Hastings 2003), another specimen was also cited and this is here considered the holotype.

*Rhapis major* was included as a synonym of *R. excelsa* by Hastings (2003) and this is followed here. Blume (1836) cited a specimen at L, but this was not found on a recent visit.

*Rhapis javanica* was included as a synonym of *R. humilis* by Hastings (2003), but the sterile type specimen, comprising two sheets at L, is clearly identifiable as *R. excelsa* based on the minute brown scales on the abaxial surface of the segments.

*Rhapis divaricata* was placed as a synonym of *R. excelsa* by Hastings (2003), and this is followed here. The type specimen agrees in all character states with *R. excelsa*.

*Rhapis excelsa* is one of the most widely and commonly cultivated palms, and has been in cultivation, particularly in Japan, for many years (Bailey 1939, Yamaguchi & Barry 1974). It is not always clear if specimens are from wild or cultivated plants, but all specimens from Japan are likely to be based on cultivated plants. A specimen (*Henry 10173* at NY) from China (Yunnan), identified by Hastings (2003) as *R. excelsa* is here included in *R. humilis*.

A specimen (*Shiu Ying Hu 12934* from KUN) from a cultivated plant is recorded as having white fruits.

Subspecific variation:—*Rhapis excelsa* occurs in four areas; southern China, Hainan, northern Vietnam, and central Vietnam. Specimens from northern Vietnam are smaller than those from central Vietnam but not significantly so. Some specimens from Hong Kong are considerably smaller than others, but other ones from there are the more usual size. It is not clear if some of these smaller specimens are from cultivated plants or not.

3. *Rhapis gracilis* Burret (1930: 883). Lectotype (here designated):—CHINA. Prov. Kwangtung: Win Foo, 180 m, 3 October 1928, *S. Sin 5338* (lectotype IBSC!) (the holotype at B was destroyed)
Stems length and diameter not recorded. Leaf ligules scarcely developed; petioles 11.5(10.5–12.5) cm long, 1.7(1.3–2.0) mm wide at the apex; abaxial hastula usually complete, a low ridge separating petiole apex from costa; segments 3(2–4) per leaf; central segments elliptic, usually multi-veined, acuminate, the apices oblique, toothed, 15.2(13.8–16.5) cm long, 2.8(2.5–3.0) cm wide at midpoint, free almost to the base, the non-split basal part 0.2 cm; lateral segments 15.5(14.0–17.0) cm long, 2.1(1.7–2.4) cm wide at midpoint, the non-split basal part 0.2 cm; abaxial surface of segments with minute, brown scales, not indumentum when first exposed. Inflorescences slender, few branched, with the first branch not as large as the rest of the inflorescence; prophyll and peduncular bract narrow, tubular, not or scarcely overlapping, the inflorescences exerted apically through the bracts on a curved peduncle; rachis 3.7 cm long; rachillae filiform, usually tomentose, especially the staminate ones; proximal rachilla 2.6 cm long, 0.5 mm wide; staminate and pistillate flowers sessile; staminate and pistillate corollas with poorly developed, inturned apical lobes, these not swollen internally; filaments not recorded; fruits globose, color not recorded, 8.2 mm long, 8.2 mm diameter, borne on a pedicelliform pistillate corolla.

Distribution and habitat:—China (Guangxi, Guangdong, Hainan)(Fig. 2) in lowland forest at 540(180–900) m elevation.

Taxonomic notes:—The type locality of Rhapis gracilis is here taken to be Yunfu, Guangdong, China, whose geographical coordinates are 22° 56’N, 112° 2’E. Hastings (2003) identified a specimen (El Colani s.n. from P) from Laos as R. gracilis, but it is here included in Rhapis subtilis.

4. Rhapis humilis Blume (1836: 54). Lectotype (designated here):—JAPAN. No locality, no date, C. Thunberg sheet number 24385 (lectotype UPS n.v., UPS image!)


Stems length and diameter not recorded. Leaf ligules acute, soon disintegrating; petioles 33.9(31.7–36.0) cm long, 3.9(2.7–5.0) mm wide at the apex; abaxial hastula usually complete, a low ridge separating petiole apex from costa; segments 18(13–28) per leaf; central segments narrowly linear, usually 1–2–veined, acuminate, the apices scarcely toothed, 34.8(31.5–40.0) cm long, 1.8(1.1–2.7) cm wide at midpoint, joined at the base, the non-split basal part 7.5(5.0–10.5) cm; lateral segments 26.0 cm long, 1.8(0.8–2.4) cm wide at midpoint, the non-split basal part 3.6(2.5–5.3) cm; abaxial surface of segments without scales, not indumentose when first exposed. Inflorescences small to large, with the first branch almost as large as the rest of the inflorescence; prophyll and peduncular bract narrow, tubular, not or scarcely overlapping, the inflorescences exerted apically through the bracts on a curved peduncle; rachis 23.8(21.0–26.5) cm long; rachillae filiform, usually tomentose, especially the staminate ones; proximal rachilla 8.2(6.0–10.5) cm long, 0.9(0.9–1.0) mm wide; staminate and pistillate flowers sessile; staminate and pistillate corollas with poorly developed, inturned apical lobes, these not swollen internally; filaments not recorded; fruits globose, yellow, 7.0 mm long, 7.0 mm diameter, borne on a pedicelliform pistillate corolla.

Distribution and habitat:—China (Guangxi, Guizhou, Yunnan)(Fig. 2) in montane forest on steep, rocky slopes at 1105(915–1250) m elevation.

Taxonomic notes:—Blume established Rhapis humilis without designating a type, and Hastings (2003) considered that lectotypification was necessary. She stated that a Thunberg collection (sheet number 24385 at UPS), comprising a leaf and partial inflorescence, matched the protologue. However, she did not designate this specimen as lectotype, and instead gave a different specimen, Thunberg s.n. from L, as the type of R. humilis. In the circumstances it seems best to designate the UPS Thunberg specimen (sheet number 24385) as lectotype of R. humilis.

Rhapis multifida is here included in synonymy. The holotype at B was destroyed, and an isotype has not been found at either IBSC, KUN, or SYS, and the type is presumed destroyed. A neotype is here designated, from the same province (Guangxi) although the original type locality has not been found on maps or gazetteers.

All specimens of Rhapis humilis cited by Hastings are from cultivated plants except Morse 380 at K, but this clearly belongs to R. robusta (and is from the type locality of that species). Only one specimen (Feng 13462 at A) records fruit color, and is given as yellow, although cultivated plants of R. humilis have white fruits.

Hastings (2003) distinguished R. multifida from R. humilis based on leaf sheath fibers, inflorescence branching, and calyx lobing. Rhapis multifida was said to have leaf sheaths with coarse outer and fine inner fibers, inflorescences branching to 2 orders, and irregularly lobed calyces. Rhapis humilis was said to have leaf sheaths with similar fibers,
inflorcescences branched to 3–4 orders, and regularly lobed calyces. However, a specimen cited by Hastings as *R. multifida*, Steward 518 at A (mistakenly given as 158) has all the character states of *R. humilis*; and a specimen cited as *R. humilis*, Chow 6249 at A, has all the states of *R. multifida*. Although this last specimen lacks leaf sheaths, another from the same locality, Fang 2347 at A, has leaf sheaths with coarse outer and fine inner fibers. Hastings also used some inflorescence characters, but it has not been possible here to distinguish between “bracts large, thick, dark brown; rachis pale brown with pale brown tomentum” for *R. multifida* and “bracts of relatively medium thickness, pale brown with darker patches; rachis dark brown and bearing rusty brown tomentum” for *R. humilis*.

5. *Rhapis kebangensis* Henderson sp. nov. Type:—VIETNAM. Quang Binh: Ba Trach district, Phong Nga-Ke Bang National Park, 17°23’N, 106°13’E, 650 m., 20 October 2015, A. Henderson & Nguyen Quoc Dung 4048 (holotype FPI!, isotype NY!). (Fig. 3)

**Stems** 0.6 m long, 0.4(0.3–0.4) cm diameter. **Leaf** ligules lobed, more or less persistent; petioles 13.2(10.0–17.7) cm long, 0.9(0.8–1.1) mm wide at the apex; abaxial hastula usually incomplete, part of the petiole continuous with the costa; segments 4(3–4) per leaf; central segments lanceolate or elliptic, usually multi-veined, acuminate, the apices oblique, toothed, 12.7(10.9–16.5) cm long, 1.9(1.5–2.2) cm wide at midpoint, free almost to the base, the non-split basal part 0.3(0.2–0.4) cm; lateral segments 12.1(10.5–15.5) cm long, 0.7(0.5–0.9) cm wide at midpoint, the non-split basal part 0.3(0.2–0.3) cm; abaxial surface of segments without scales, gray indumentose when first exposed. **Inflorescences** slender, few branched, with the first branch not as large as the rest of the inflorescence; prophyll and peduncular bract narrow, tubular, not or scarcely overlapping, the inflorescences exerted apically through the bracts on a curved peduncle; rachis 2.4(2.2–2.5) cm long; rachillae not filiform, glabrous; proximal rachilla 5.6(4.7–6.5) cm long, 0.8(0.6–0.9) mm wide; staminate and pistillate flowers sessile; staminate and pistillate corollas with well developed, erect, triangular apical lobes, these swollen internally; filaments terete; **fruits** globose, color not recorded, 7.8(5.6–9.9) mm long, 5.7(4.8–6.6) mm diameter, borne on a swollen, persistent perianth.

**Distribution and habitat:**—Vietnam (Quang Binh)(Fig. 4) at the base of steep, limestone cliffs at 593(450–680) m elevation.

**Taxonomic notes:**—*Rhapis kebangensis* is unique in the genus by its segments with the abaxial surface gray indumentose when first exposed. The swollen, persistent perianth of this species is much more developed than those of similar species (e.g., *R. subtilis*). The type specimen is unusual in having two inflorescences, one pistillate and one staminate.


**Stems** 2.2(1.0–3.2) m long, 0.7(0.4–1.0) cm diameter. **Leaf** ligules lobed, more or less persistent; petioles 34.3(7.5–69.5) cm long, 2.6(1.6–3.9) mm wide at the apex; abaxial hastula usually complete, a low ridge separating petiole apex from costa; segments 8(2–13) per leaf; central segments lanceolate or elliptic, usually multi-veined, acuminate, the apices oblique, toothed, 29.3(18.5–41.0) cm long, 3.7(1.5–7.0) cm wide at midpoint, joined at the base, the non-split basal part 4.1(1.6–8.8) cm; lateral segments 26.8(15.0–39.0) cm long, 2.4(1.0–4.3) cm wide at midpoint, the non-split basal part 2.2(1.0–5.4) cm; abaxial surface of segments without scales, not indumentose when first exposed. **Inflorescences** small to large, with the first branch almost as large as the rest of the inflorescence; prophyll and peduncular bract broad, flattened, completely overlapping, the inflorescences exerted laterally through the bracts on a recurved peduncle; rachis 8.1(5.4–14.0) cm long; rachillae not filiform, glabrous; proximal rachilla 6.0(3.8–10.2) cm long, 1.3(0.8–2.6) mm wide; staminate and pistillate flowers sessile; staminate and pistillate corollas with poorly developed, inturned apical lobes, these not swollen internally; filaments terete; **fruits** globose, white, 8.3(7.2–9.7) mm long, 6.7(5.5–7.8) mm diameter, borne on a swollen, persistent perianth.

**Taxonomic notes:**—Hastings (2003) reported one specimen as having hermaphrodite flowers (see also Giddey et al., 2009). The range of *Rhapis lasonis* is divided into two lowland populations—west (Laos, Thailand) and east (Vietnam) of the higher elevation Truong Son range. Specimens from Laos and Thailand differ significantly from those from Vietnam in ten variables (stem diameter, petiole length, petiole width, number of segments, length of central segment, non-split part of central segment, length of lateral segment, non-split part of lateral segment, rachis length, proximal rachilla length) (t-test, P <0.05), with specimens from Vietnam having higher mean values for all variables. Based this, the two populations are recognized as subspecies (subsp. laosensis, macrantha).
Key to the subspecies of *Rhapis laosensis*

1. Petioles 28.0(7.5–52.0) cm long; central segments 23.9(18.5–29.8) cm long; central Laos and eastern Thailand ... subsp. *laosensis*
   - Petioles 39.8(21.0–69.5) cm long; central segments 32.3(21.2–41.0) cm long; central Vietnam......................... subsp. *macrantha*

6a. *Rhapis laosensis* subsp. *laosensis*

Petioles 28.0(7.5–52.0) cm long; central segments 23.9(18.5–29.8) cm long.

**Distribution and habitat:**—Central Laos and eastern Thailand (Fig. 4) in lowland forest at 329(100–600) m elevation.

6b. *Rhapis laosensis* subsp. *macrantha* (Gagnepain) Henderson **comb. & stat. nov.**


Petioles 39.8(21.0–69.5) cm long; central segments 32.3(21.2–41.0) cm long.

**Distribution and habitat:**—Central Vietnam (Fig. 4) in lowland forest and persisting in disturbed areas, often on limestone soils, at 244(20–1000) m elevation.

   **Lectotype** (designated by Hastings 2003):—VIETNAM. Dong Ban mountains, Kien Khe 19 April 1884, *H.*-F. Bon 2345 (lectotype P!, isolectotype FI!)

Stems 1.8(1.5–2.0) m long, 0.8(0.7–0.8) cm diameter. Leaf ligules acute, soon disintegrating; petioles 37.0(20.5–73.0) cm long, 2.6(1.8–3.3) mm wide at the apex; abaxial hastula usually complete, a low ridge separating petiole apex from costa; segments 8(5–13) per leaf; central segments lanceolate or elliptic, usually multi-veined, acuminate, the apices oblique, toothed, 26.9(18.0–35.0) cm long, 3.0(2.2–4.2) cm wide at midpoint, free almost to the base, rarely joined at the base, the non-split basal part 0.7(0.1–2.5) cm; lateral segments 23.8(17.0–32.5) cm long, 1.8(1.0–3.6) cm wide at midpoint, the non-split basal part 0.6(0.1–1.7) cm; abaxial surface of segments without scales, not indumentose when first exposed. **Inflorescences** small to large, with the first branch almost as large as the rest of the inflorescence; prophyll and peduncular bract narrow, tubular, not or scarcely overlapping, the inflorescences exerted apically through the bracts on a curved peduncle; rachis 15.9(10.0–20.0) cm long; rachillae filiform, usually tomentose, especially the staminate ones; proximal rachilla 6.9(3.3–10.7) cm long, 0.7(0.4–1.2) mm wide; staminate and pistillate flowers sessile; staminate and pistillate corollas with poorly developed, inturned apical lobes, these not swollen internally; filaments terete; **fruits** globose, white, 7.5(6.1–8.5) mm long, 6.8(6.3–7.4) mm diameter, borne on a pedicelliform pistillate corolla.

**Distribution and habitat:**—Northern Vietnam (Ninh Binh, Thanh Hoa)(Fig. 4) in lowland forest on limestone outcrops at 200(100–300) m elevation.

**Taxonomic notes:**—One specimen (Spire 5929 at P) is labeled from Laos, and apparently from a place called ‘Ko San’. It is determined by Hastings as *R. micrantha* and appears to represent that species. The locality has not been found on maps or gazetteers. According to Gagnepain (1943), Spire collected around Luang Prabang in Laos.


Stems 1.2 m long, 0.4 cm diameter. Leaf sheath fibers coarse, flattened, forming a diagonal mesh, extended into a well-developed ligule; petioles 14.8(14.0–15.5) cm long, 1.5(1.3–1.5) mm wide at the apex; abaxial hastula usually incomplete, part of the petiole continuous with the costa; segments 15(15–16) per leaf; central segments narrowly linear, usually 1–2-veined, acuminate, the apices scarcely toothed, 13.6(13.2–14.0) cm long, 0.6(0.5–0.7) cm wide at midpoint, joined at the base, the non-split basal part 5.2(4.3–6.0) cm; lateral segments 12.4(12.0.12.7) cm long, 0.6(0.5–0.6) cm wide at midpoint, the non-split basal part 3.4(3.0–3.7) cm; abaxial surface of segments without scales, not indumentose when first exposed. **Inflorescences** slender, few branched, with the first branch not as large as the rest of the inflorescence; prophyll and peduncular bract narrow, tubular, not or scarcely overlapping, the inflorescences
exerted apically through the bracts on a curved peduncle; rachis 8.3(7.5–9.0) cm long; rachillae filiform, usually tomentose, especially the staminate ones; proximal rachilla 3.2(3.0–3.5) cm long, 0.3(0.3–0.4) mm wide; staminate and pistillate flowers pedicellate; staminate and pistillate corollas with poorly developed, inturned apical lobes, these not swollen internally; filaments not recorded; fruits color and size not recorded, borne on a pedicilliform pistillate corolla.

**Distribution and habitat:**—Vietnam (Nghe An)(Fig. 4) in lowland forest on limestone soils at 275(250–300) m elevation.

**FIGURE 4.** Distribution maps of *Rhapis kebangensis*, *R. laosensis*, *R. micrantha*, and *R. puhuongensis*. 

**Taxonomic notes:**—By its incomplete abaxial hastula, narrow segments, and pedicilliform pistillate corolla, *Rhapis puhuongensis* appears most similar to *R. vidalii*. It differs from that species in its segments that are joined at the base.

9. *Rhapis robusta* Burret (1937: 587). Lectotype (here designated):—CHINA. Kwangsi: Lungchow, 7 July 1935, S. Ko 55429 (lectotype IBSC!)(the holotype at B was destroyed)

**Stems** 1.5 m long, 0.7(0.6–0.8) cm diameter. **Leaf** sheath fibers coarse, flattened, forming a diagonal mesh, extended
into a well-developed ligule; petioles 29.7(20.0–43.0) cm long, 2.2(1.7–3.0) mm wide at the apex; abaxial hastula usually complete, a low ridge separating petiole apex from costa; segments 5(2–8) per leaf; central segments elliptic, usually multi-veined, acuminate, the apices oblique, toothed, 21.5(15.7–27.0) cm long, 3.1(1.8–4.2) cm wide at midpoint, joined at the base, the non-split basal part 3.3(1.4–5.3) cm; lateral segments 19.8(15.7–24.0) cm long, 2.2(1.9–2.7) cm wide at midpoint, the non-split basal part 1.9(1.0–2.7) cm; abaxial surface of segments without scales, not indumentose when first exposed. Inflorescences slender, few branched, with the first branch not as large as the rest of the inflorescence; prophyll and peduncular bract narrow, tubular, not or scarcely overlapping, the inflorescences exerted apically through the bracts on a curved peduncle; rachis length not recorded; rachillae filiform, usually tomentose, especially the staminate ones; proximal rachilla 6.2(4.0–7.4) cm long, 0.6(0.4–0.8) mm wide; staminate and pistillate flowers sessile; staminate and pistillate corollas with poorly developed, inturned apical lobes, these not swollen internally; filaments keeled; fruits color and size not recorded, borne on a pedicelliform pistillate corolla.

Distribution and habitat:—Northern Vietnam (Cao Bang, Ha Giang) and adjacent China (Guangxi)(Fig. 5) in lowland forest on limestone soils at 500(400–700) m elevation.

FIGURE 5. Distribution maps of Rhapis robusta, R. subtilis subsp. subtilis, R. subtilis subsp. siamensis, and R. vidalii.

Taxonomic notes:—The segments of Rhapis robusta have scarcely toothed apices and they appear almost acuminate.

Stems 2.1(1.3–2.5) m long, 0.6(0.3–1.0) cm diameter. Leaf ligules lobed, more or less persistent; petiolo 28.6(7.0–52.5) cm long, 1.9(1.1–2.8) mm wide at the apex; abaxial hastula usually incomplete, part of the petiolo continuous with the costa, sometimes complete, a low ridge separating petiolo apex from costa; segments 7(2–11) per leaf; central segments lanceolate or elliptic, usually multi-veined, acuminate, the apices oblique, toothed, 22.3(9.0–33.0) cm long, 2.9(1.2–7.0) cm wide at midpoint, free almost to the base or sometimes joined at the base, the non-split basal part 2.0(0.2–6.0) cm; lateral segments 20.4(8.2–29.0) cm long, 1.6(0.6–3.8) cm wide at midpoint, the non-split basal part 1.3(0.3–2.7) cm; abaxial surface of segments without scales, not indumentose when first exposed. Inflorescences slender, few branched, with the first branch not as large as the rest of the inflorescence; prophyll and peduncular bract narrow, tubular, not or scarcely overlapping, the inflorescences exerted apically through the bracts on a curved peduncle; rachis 4.5(1.0–12.8) cm long; rachillae not filiform, glabrous; proximal rachilla 9.8(2.8–15.5) cm long, 1.2(0.7–2.0) mm wide; staminate and pistillate flowers sessile; staminate and pistillate corollas with well developed, erect, triangular apical lobes, these swollen internally; filaments terete; fruits globose, white, 7.5(6.0–9.4) mm long, 6.1(5.6–7.1) mm diameter, borne on swollen, persistent perianth.

Taxonomic notes:—Two qualitative variables (abaxial hastula and central segment splitting) were found to be polymorphic within *Rhapis subtilis* (as a preliminary species). However, splitting the preliminary species into several consistent species, as described in the Materials and Methods section, was found to give improbable results, and no corroborating evidence that these were separate taxa was found (no geographic separation, no quantitative differences). Therefore, *R. subtilis* is recognized as a phylogenetic species with two variables treated as traits.

Subspecific variation:—Specimens of *Rhapis subtilis* come from two separate areas—a southern one in Peninsular Thailand and a northern one in south-central Thailand, central Laos, and western Cambodia. Specimens from the southern area differ from those from the northern one in eight quantitative variables (stem diameter, petiolo length, number of segments, length of central segment, non-split part of central segment, length of lateral segment, rachis length, proximal rachilla length) (<0.05), with specimens from the southern area having higher mean values for all variables. Based on this, the two are recognized as subspecies (subsp. *siamensis*, *subtilis*). Lacking enough data for testing, the two, incomplete specimens from Sumatra are included in subsp. *siamensis*.

Key to the subspecies of *Rhapis subtilis*

1. Abaxial hastula usually incomplete, part of the petiolo continuous with the costa; central segments 18.2(9.0–23.5) cm long, free almost to the base or joined at the base; south-central Thailand, central Laos, and western Cambodia..................subsp. *subtilis*
- Abaxial hastula usually complete, a low ridge separating petiolo apex from costa; central segments 25.2(14.5–33.0) cm long, joined at the base, rarely free almost to the base; Peninsular Thailand and western Sumatra..........................subsp. *siamensis*

10a. *Rhapis subtilis* subsp. *subtilis*

Abaxial hastula usually incomplete, part of the petiolo continuous with the costa; central segments 18.2(9.0–23.5) cm long, free almost to the base or joined at the base.

Distribution and habitat:—Central Laos, south-central Thailand, and western Cambodia (Fig. 5) in lowland forest or riparian forest on granitic soils at 219(30–500) m elevation.

Taxonomic notes:—The type specimen of *Rhapis subtilis*, from central Laos, as well as another specimen (*El Colani s.n.* at P) from near there are here considered conspecific with specimens from further south in Thailand and Cambodia. However, these two northern, outlying specimens differ somewhat from those from further south in their shorter petioles and less numerous segments which are free to the base (versus usually joined at the base). More specimens from central Laos are needed to test for differences between the two populations.

Hodel (1998) noted that subsp. *subtilis* (as *R. subtilis*) occurs in riparian or rheophytic habitats on granite soils and forms tight clumps, whereas subsp. *siamensis* (as *R. siamensis*) occurs on limestone rocks and forms loose colonies by rhizomes.

Abaxial hastula usually complete, a low ridge separating petiole apex from costa; central segments 25.2(14.5–33.0) cm long, joined at the base, rarely free almost to the base.

**Distribution and habitat:**—Peninsular Thailand and western Sumatra (Fig. 5) in lowland forest on limestone outcrops at 148(20–250) m elevation.

*Type:*—VIETNAM. Hoa Binh: Mai Chau district, Van Mai municipality, highway 7, 15 km post, between 20°35’N, 105°02’E and 20°34’N, 105°02’E, 300–350 m, 12 December 2002, D. Harder, N. T. Hiep, L. Averyanov, DKH 8123 (holotype HN n.v., isotype LE n.v.)

**Stems** 1.1(0.9–1.3) m long, 0.3(0.2–0.3) cm diameter. **Leaf** sheath fibers coarse, flattened, forming a diagonal mesh, extended into a well-developed ligule; petioles 17.3(11.0–26.5) cm long, 1.0(0.8–1.2) mm wide at the apex; abaxial hastula usually incomplete, part of the petiole continuous with the costa; segments 7(5–9) per leaf; central segments narrowly linear, usually 1–2-veined, acuminate, the apices scarcely toothed, 16.8(14.2–22.0) cm long, 0.7(0.4–1.2) cm wide at midpoint, free almost to the base, the non-split basal part 0.3(0.2–0.7) cm; lateral segments 15.9(13.0–20.5) cm long, 0.6(0.4–1.4) cm wide at midpoint, the non-split basal part 0.3(0.2–0.4) cm; abaxial surface of segments without scales, not indumentose when first exposed. **Inflorescences** slender, few branched, with the first branch not as large as the rest of the inflorescence; prophyll and peduncular bract narrow, tubular, not or scarcely overlapping, the inflorescences exerted apically through the bracts on a curved peduncle; rachis 4.4(2.0–6.7) cm long; rachillae filiform, usually tomentose, especially the staminate ones; proximal rachilla 3.0 cm long, 0.3 mm wide; staminate and pistillate flowers pedicellate; staminate and pistillate corollas with poorly developed, inturned apical lobes, these not swollen internally; filaments terete; **fruits** globose, white, 9.1(8.9–9.3) mm long, 7.4(7.0–7.7) mm diameter, borne on a pedicelliform pistillate corolla.

**Distribution and habitat:**—Northern Vietnam (Hoa Binh, Thanh Hoa) (Fig. 5) in lowland forest on limestone outcrops at 647(400–800) m elevation.

**Taxonomic notes:**—By its incomplete abaxial hastula, narrow segments, and pedicelliform pistillate corolla, *Rhapis vidalii* appears most similar to *R. puhuongensis*. It differs from this species in its segments free almost to the base.

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### Appendix 1. Qualitative and quantitative variables

Abbreviations in parentheses at the end of each character are the column labels in the Data Matrix (http://sciweb.nybg.org/Science2/res/Henderson/Rhapis.xls.zip).

**Qualitative characters**

1. Ligules scarcely developed (0); ligules lobed, more or less persistent (1); ligules acute, solid, more or less persistent (2); ligules acute, soon disintegrating (3). (ligules)

2. Abaxial hastula usually complete, a low ridge separating petiole apex from costa (0); abaxial hastula usually incomplete, part of the petiole continuous with the costa (1). (hastula)

3. Central segments lanceolate or elliptic, usually multi-veined, acuminate, the apices oblique, toothed (0); central
segments linear-lanceolate, usually multi-veined, not acuminate, the apices truncate, toothed (1); central segments narrowly linear, usually 1–2-veined, acuminate, the apices scarcely toothed (2). (centseg)

4. Central segments free almost to the base (0); central segments joined at the base (1). (joined)

5. Abaxial surface of segments with minute, brown scales (0); abaxial surface of segments without scales (1). (scales)

6. Abaxial surface of segments gray indumentose when first exposed (0); abaxial surface of segments not indumentose when first exposed (1) (indume)

7. Inflorescences small to large, with the first branch almost as large as the rest of the inflorescence (0); inflorescences slender, few branched, with the first branch not as large as the rest of the inflorescence (1). (inflor)

8. Prophyll and peduncular bract narrow, tubular, not or scarcely overlapping, the inflorescences exerted apically through the bracts on a curved peduncle (0); prophyll and peduncular bract broad, flattened, completely overlapping, the inflorescences exerted laterally through the bracts on a recurved peduncle (1). (bracts)

9. Rachillae filiform, usually tomentose, especially the staminate ones (0); rachillae not filiform, glabrous (1). (rachil)

10. Staminate and pistillate flowers pedicellate (0); staminate and pistillate flowers sessile (1). (pedicel)

11. Staminate and pistillate corollas with poorly developed, inturned apical lobes, these not swollen internally (0); staminate and pistillate corollas with well developed, erect, triangular apical lobes, these swollen internally (1). (tubular)

12. Filaments keeled (0); filaments terete (1). (filament)

13. Fruits borne on a pedicelliform pistillate corolla (0); fruits borne on a swollen, persistent perianth (1). (pediform)

Quantitative variables

1. Stem height, from label data (m) (stemheight)
2. Stem diameter, without sheaths, from specimens (cm) (stemdiameter)
3. Petiole length (cm) (petiole)
4. Petiole width at petiole apex (mm) (petiolewid)
5. Number of segments per leaf (segments)
6. Length of central segment (cm) (lencenseg)
7. Width of central segment at middle (cm) (widcenseg)
8. Length of non-split, basal part of central segments (cm) (nonsplit)
9. Length of lateral segment (cm) (lenlatseg)
10. Width of lateral segment at middle (cm) (widlatseg)
11. Length of non-split, basal part of lateral segments (cm) (nonsplitlat)
12. Rachis length (cm) (rachlen)
13. Proximal rachilla length (cm) (proxraclen)
14. Proximal rachilla width (mm) (proxracwid)
15. Fruit length (mm) (fruitlen)
16. Fruit diameter (mm) (fruitwid)

Excluded Names

Rhapis arundinacea Aiton (1789: 474) = Sabal minor (Jacquin) Persoon.

Rhapis cochinchenensis (Loureiro) Martius (1838: 254). Based on a possible mixed specimen, see Hastings (2003).

Rhapis caroliniana hort. ex Kunth (1841: 3) = Sabal minor (Jacquin) Persoon.

Rhapis cordata hort. ex Baxter (1850: 624). Nomen nudum.


Rhapis grossifibrosa Gagnepain (1937: 159) = Guithia grossifibrosa (Gagnepain) Dransfield, Lee & Wei.

Rhapis kwamwontzik Wendland (1854: 34). Nomen nudum.


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