A monograph of *Cyrtostachys* (Arecaceae)

Charlie D. Heatubun^{1,4}, William J. Baker², Johanis P. Mogea³, Madeline M. Harley², Sri S. Tjitrosoedirdjo⁴ & John Dransfield²

Summary. Cyrtostachys Blume (Areceae: Arecaceae) is treated in this study as a genus of tree palms with a disjunct distribution pattern across Malesia and consisting of seven species. Three species are newly recognised (*C. bakeri* Heatubun, *C. barbata* Heatubun and *C. excelsa* Heatubun). Five previously accepted species (*C. brassii* Burret, *C. kisu* Becc., *C. microcarpa* Burret, *C. peekeliana* Becc. and *C. phanerolepis* Burret) are reduced to synonymy with *C. loriae* Becc. and one species (*C. compsoclada* Burret) is removed to Heterospathe as Heterospathe compsoclada (Burret) Heatubun, while *C. ledermanniana* Becc. is considered as a doubtful taxon. A determination key is presented and detailed descriptions provided for all taxa. A phylogenetic analysis of all species in the genus was performed based on morphological data. Despite the poorly resolved tree topologies, *Cyrtostachys* is resolved as monophyletic, with *C. glauca* H. E. Moore as sister to all other species, and the west Malesian species *C. renda* Blume probably representing a dispersal from within a Papuasian clade into the Sunda shelf. Natural history observations, including uses and conservation status are also presented in this monograph.

Key Words. Arecaeae, Arecaeae, Arecoideae, *Cyrtostachys*, Malesia, morphology, taxonomy.

Introduction

Cyrtostachys Blume is a genus of palms described almost 170 years ago by Blume (1838), based on the remarkable species, C. renda Blume, the sealing wax palm, a species well-known for its brilliant red leaf sheaths. The genus is highly desirable from a horticultural point of view and it is also used locally for a variety of purposes; the extraordinary disjunct distribution poses interesting biogeographic questions that can only be addressed when its interspecific relationships are better understood.

Cyrtostachys has a disjunct distribution pattern (Map 1), with one species (C. renda) occurring to the west of Wallace's line in south Thailand, Malay Peninsula, Sumatra and Borneo, and the remaining six species on the island of New Guinea to the Solomon Islands (Moore 1973; Dransfield 1981, 1987; Baker et al. 1998). Cyrtostachys belongs to subfamily Arecoideae and tribe Areceae based on its pinnate, reduplicate leaf, monoecy with flowers borne in triads of a central pistillate and two lateral staminate flowers. It can be distinguished from other genera of arecoid palm by the

strongly divaricate inflorescence branches, flowers borne in pits along the rachillae, connate petals and more than six stamens in staminate flowers (Uhl & Dransfield 1987). Dransfield & Uhl (1986) placed Cyrtostachys in its own subtribe, Cyrtostachydinae, as an isolated genus with no clear relatives. Moreover, in most studies (Asmussen & Chase 2001; Lewis & Doyle 2002; Hahn 2002; Essig & Litten 2004) no clear affinities with other palm genera have been found, apart from establishing that *Cyrtostachys* belongs to the large group of Indo-Pacific pseudomonomerous arecoid palm genera tribe Areceae (sensu Dransfield et al. 2005, 2008). Recently, a phylogenetic analysis of all genera of Areceae based on low-copy nuclear DNA provided moderate support for a relationship between Cyrtostachys and Clinostigma (Norup et al. 2006). However, further evidence is required to substantiate this position. Thus, in the new phylogenetic classification of the palm family (Arecaceae), Cyrtostachys remains as an unplaced member of Areceae (Dransfield et al. 2005, 2008).

Although the genus *Cyrtostachys* is well circumscribed, the species, with the exception of *C. renda*, are as yet

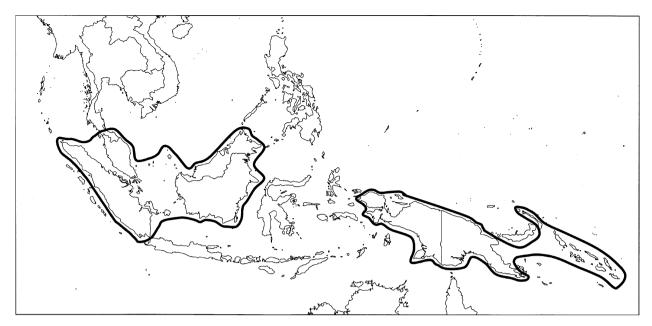
Accepted for publication July 2008.

¹ Faculty of Forestry, Universitas Papua, Jl. Gunung Salju, Amban, Manokwari 98314, Papua Barat, Indonesia. e-mail: charlie_deheatboen@yahoo.com

² Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB, UK.

³ Herbarium Bogoriense, Puslitbang Biologi LIPI, Jl. Ir. H. Juanda No. 22, Bogor, Jawa Barat, Indonesia.

⁴ Biology Department, Sekolah Pascasarjana Institut Pertanian Bogor, Baranangsiang, Bogor, 16680, Jawa Barat, Indonesia.



Map 1. Distribution map of the genus Cyrtostachys Blume.

rather poorly known. Most of these Papuasian species were described based on single specimens (Beccari 1905, 1914b, 1923; Burret 1936, 1937, 1939; Moore 1966). No monographic account has ever been published (Uhl & Dransfield 1987; Barfod *et al.* 2001). Infraspecific taxa have been described from cultivation (Tucker 1992; Ellison & Ellison 2001; Waddel 2002), and the number of these could increase in parallel to horticultural demand. The genus is thus in need of reassessment.

In the 40 years since the last species, *Cyrtostachys glauca* H. E. Moore, was published (Moore 1966) the number of herbarium specimens of *Cyrtostachys* has increased greatly, particularly due to activities related to the *Palms of New Guinea* Project (Baker 2000, 2002); the palm collecting density in the western part of New Guinea, in particular, has increased dramatically. Now we have sufficient materials in the herbarium, field experience, and access to new data (anatomy and pollen morphology) to study the genus and appreciate the wide range of variation within it. Furthermore, there has also been success in tracing isotypes of Burret's species, the holotypes of which were destroyed during the Second World War in Berlin.

This monograph aims to provide a modern taxonomic treatment of *Cyrtostachys* and to compile and reevaluate published information on its systematics, natural history, uses and conservation status.

Taxonomic History

The genus *Cyrtostachys* was described for the first time by Carl Ludwig von Blume in 1838 based on *C. renda* Blume (Blume 1838). Blume had intended to publish the genus in *Rumphia*, but publication of his great

work was delayed until 1843 (Stafleu & Cowan 1976). In notes with the protologue, he wrote: "...in *Rumphia l.c.*" behind the genus name and he provided only a brief description of the genus and species while in *Rumphia* he provided a full description of the genus and species accompanied by a plate with details of *C. mnda* from a specimen collected by Korthals near Indrapura in Sumatra. The word *Cyrtostachys* comes from the Greek word *cyrtos* (arched) and *stachys* (a spike) in reference to the recurved inflorescence (Whitmore 1973; Jones 1995).

Odoardo Beccari (1905) published the second species of the genus, Cyrtostachys loriae Becc., based on a Hartmann collection from the Owen Stanley Range, Papua New Guinea, and this was followed by C. kisu Becc. (Beccari 1914a), based on a specimen from the Solomon Islands made by Guppy and C. peekeliana Becc. (Beccari 1914b) from New Ireland (Papua New Guinea) based on a collection made by Peekel. In 1923 another species was published by Beccari, C. ledermanniana Becc. to accommodate Ledermann's specimen from Ettapenberg, Papua New Guinea (Beccari 1923). Max Burret published C. brassii Burret (Burret 1935) based on a specimen collected by L. J. Brass from Kubuna, Central Division, Papua New Guinea. Two more species of Cyrtostachys (C. phanerolepis Burret and C. compsoclada Burret) were published by Burret (1936). The last of Burret's species, C. microcarpa Burret, was published in 1939 and based on a L. J. Brass specimen from Lake Daviambu, Fly River, Papua New Guinea (Burret 1939). Harold E. Moore Jr discovered and published C. glauca H. E. Moore from Morobe district, Papua New Guinea (Moore 1966).

Materials and Methods

Morphology

Morphology and distribution of the species were studied based on specimens (dried and spirit-preserved materials) deposited at A, AAU, BH, BO, BRI, FI, K, KEP, L, LAE, MAN, PNH, SAN, and SING (Holmgren et al. 1990). Many new specimens have been collected recently by the authors. In particular, new specimens were collected in western New Guinea (Indonesian province of Papua and Irian Jaya Barat) by the first author in 1998 – 2005. Specimens were made in the field using standard preparation guidelines proposed by Dransfield (1986). Collections of leaf samples, inflorescence (rachillae with flowers in bud and/or at anthesis), and mature fruits were preserved in 70% alcohol for further studies.

Measurements were taken from spirit-preserved material and dried herbarium specimens and from cultivated individuals. Floral parts were measured from spirit-preserved material or dried specimens rehydrated by boiling.

Pollen Morphology

Pollen material was obtained from dried herbarium specimens and spirit-preserved material. Seventeen samples were chosen to represent the wide range of taxa in the genus *Cyrtostachys*. Details of pollen preparation and methods for herbarium material follow Harley (1990, 1996) and terminology follows Punt *et al.* (1994), Harley (1999) and Harley & Baker (2001). Microphotographs were taken using a Nikon D100 Optiphot light microscope (LM) and a Hitachi S-2400 scanning electron microscope (SEM).

Phylogenetic Analysis

A preliminary phylogenetic analysis of all species of *Cyrtostachys* was conducted. In recent molecular phylogenetic studies, *Cyrtostachys* is resolved in a position sister to a clade including *Nenga* and *Areca* (Asmussen & Chase 2001), or *Areca* (Hahn 2002), or *Iguanura* (Lewis &

Doyle 2002). Based on histological studies of the fruit (Essig & Litten 2004) the genus has some similarities with *Hydriastele*. Therefore, in our analysis we have included *Areca catechu* L., *Hydriastele costata* F. M. Bailey, *Pinanga rumphiana* (Mart.) J. Dransf. & Govaerts and *Rhopaloblaste ledermanniana* Becc. as outgroups. Seventeen morphological and palynological characters were included in the data matrix (Table 1), which was constructed in MacClade 4.0 (Maddison & Maddison 2000). A parsimony analysis was performed using PAUP 4.0b10 (Swofford 1998). All characters were treated as unordered and were equally weighted. Support for the clades was calculated by conducting a 10,000 replicate bootstrap analysis using the branch and bound algorithm.

Character List

General Habit Characters

- 1. Habit: solitary (0), clustering (1). This character has been discussed in detail by Holttum (1955), Dransfield (1978), Uhl & Dransfield (1987), Tomlinson (1990) and Fisher & Maidman (1999) not only for descriptive terminology, but also for developmental physiology and its value for systematics.
- 2. Crown shape: spherical (0), hemispherical (1), shuttle-cock shaped (2). The crown shape is an obvious character and very helpful in recognising species in the field. The crown itself is composed of many leaves and forms a distinctive shape in outline. A spherical shape is formed when leaves spread out in all directions, forming a circular outline when viewed from a distance. A hemispherical shape is formed when the lowest leaves make angles 15° above or below the horizontal or leaf inclination is $\pm 30^{\circ}$, taking into account the angles of the lowest leaves either side of the horizontal. The shuttle-cock crown arises when the inclination of the lowest leaves is more than 30° above horizontal.
 - 3. Leaflet arrangement: regular (0), irregular (1).
 - 4. Leaflet thickness: papery (0), leathery (1).
- 5. Ramenta on abaxial surface of leaflet: absent (0), present (1).

Table 1. Data matrix for phylogenetic analysis of morphological and palynological data of species of *Cyrtostachys* and outgroups. Inapplicable characters (–) are indicated. For polymorphic characters, both states are shown.

Terminal taxa	Characters																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Cyrtostachys bakeri	1	2	0	1	1	0	0	0	1	3	1	1	1	1	3	1	0
Cyrtostachys barbata	0	1	0	1	1	1	0	0	1	3	0	1	1	1	3	1	0
Cyrtostachys elegans	1	1	0	0	1	0	0	0	1	4	1	1	1	1	3	1	0
Cyrtostachys excelsa	0	2	1	1	0	0	0	0	1	4	1	1	1	1	3	1	0
Cyrtostachys glauca	1	0	0	0	1	0	1	_	1	3	0	1	1	1	3	0	0
Cyrtostachys loriae	0	1	0	1	1	0	0	0	1	3	1	1	1	1	3	1	0
Cyrtostachys renda	1	2	0	0	1	0	0	1	1	3	0/1	1	1	1	2	1	0
Areca catechu	0	2	0	0	0	_	0	0	0	2	0	0	0	0	0	0	1
Hydriastele costata	0	0	0	0	0	_	0	_	0	3	0	0	0	0	1	0	1
Pinanga rumphiana	0	1	0	0	0	_	0	0	0	1	0	0	0	0	1	0	1
Rhopaloblaste ledermanniana	0	0	0	0	1	0	0	_	1	4	0	0	0	0	1	0	1

- 6. Arrangement of ramenta: separate (0), continuous/ connected (1).
 - 7. Leaf sheath surface: not glaucous (0), glaucous (1).
 - 8. Crownshaft colour: green (0), red (1).

General Reproductive Characters

- 9. Inflorescence basal branches: not strongly divaricate (0), strongly divaricate (1). The strongly divaricate inflorescence is defined based on the angle formed between the first primary branch and the rachis (main axis) being more than 45°.
- 10. Inflorescence branching orders: spicate (0), 1 branching order (1), 2 branching orders (2), 3 branching orders (3), 4 branching orders (4).
 - 11. Rachilla pits: superficial pits (0), deep pits (1).
- 12. Pistillate calyx persistent on rachilla: absent (0), present (1).
 - 13. Petals in male flowers: free (0), connate (1).
 - 14. Filaments in male flowers: free (0), connate (1).

Pollen Characters

- 15. Pollen tectum surface: reticulate (0), perforate (1), rugulate (2), verrucate-gemmate (3).
 - 16. Trichotomosulcate grains: absent (0), present (1).

Seed Character

17. Seed endosperm: homogenous (0), ruminate (1).

Conservation Status

The conservation status of each species of the genus Cyrtostachys was assessed based on the IUCN red list categories and criteria version 3.1 (IUCN 2001).

Results and Discussion

Species Delimitation

A morphological species concept (Davies & Heywood 1963; McDade 1995; Dransfield 1999) is used in this monograph. Like Barrow (1998), we also looked at the constancy of morphological character states both within and between populations and recognised as species only those smallest units which can be diagnosed by constant character states.

Seven taxa of Cyrtostachys are recognised in this monograph (Table 2); three species are new (C. bakeri Heatubun, C. excelsa Heatubun and C. barbata Heatubun); five taxa (C. brassii Burret, C. kisu Becc., C. microcarpa Burret, C. peekeliana Becc. and C. phanerolepis Burret) are treated as new synonyms of C. loriae Becc. and one taxon (C. compsoclada Burret) is incorrectly described in Cyrtostachys and is transferred to Heterospathe. One species, C. ledermanniana Becc., is regarded as an imperfectly known taxon. For full discussion see Taxonomic Treatment.

Morphology

Of the seven species of Cyrtostachys, three species are solitary (C. excelsa, C. loriae and C. barbata) and four others are clustering (C. bakeri, C. elegans, C. glauca, and C. renda). However, although generally solitary, some populations of C. loriae in Indonesia, Province of Papua, are clustering. Furthermore, C. renda also displays variation in habit character, especially in individuals in cultivation.

Table 2. Comparison of previously recognised taxa in Cyrtostachys with taxa recognised in this monograph. Synonyms names are shown in italics.

Species of Cyrtostachys accepted in World checklist (Govaerts & Dransfield 2005)

Species of Cyrtostachys accepted in this monograph

Cyrtostachys elegans Burret Cyrtostachys glauca H. E. Moore Cyrtostachys loriae Becc. Cyrtostachys brassii Burret Cyrtostachys kisu Becc.

Cyrtostachys microcarpa Burret Cyrtostachys peekeliana Becc.

Cyrtostachys phanerolepis Burret

Cyrtostachys renda Blume

Areca erythropoda Miq. Cyrtostachys lakka Becc.

Cyrtostachys ledermanniana Becc.

Cyrtostachys compsoclada Burret

Cyrtostachys bakeri Heatubun sp. nov. Cyrtostachys barbata Heatubun sp. nov. Cyrtostachys elegans Burret

Cyrtostachys excelsa Heatubun sp. nov. Cyrtostachys glauca H. E. Moore

Cyrtostachys loriae Becc.

Cyrtostachys brassii Burret synon. nov. Cyrtostachys kisu Becc. synon. nov. Cyrtostachys microcarpa Burret synon. nov. Cyrtostachys peekeliana Becc. synon. nov.

Cyrtostachys phanerolepis Burret synon. nov.

Cyrtostachys renda Blume Areca erythropoda Miq. Cyrtostachys lakka Becc. Cyrtostachys lakka var. singaporensis Becc.

Imperfectly known (doubtful) taxon: Cyrtostachys ledermanniana Becc.

Excluded Taxon: Heterospathe compsoclada (Burret) Heatubun comb. nov.

Species of *Cyrtostachys* are moderate to robust palms with stems from 10 to 30 m high, they are entirely unarmed, pleonanthic and monoecious palms and grow in various conditions from tropical lowland rainforest to montane forest (900 m a.s.l.); sometimes they emerge above the forest canopy. The palm architecture of this genus conforms to Corner's model for solitary species and Tomlinson's model for clustering species (Hallé *et al.* 1976; Dransfield 1978; Tomlinson 1990; Uhl & Dransfield 1987).

Stem

The stem of Cyrtostachys varies from moderate (5.5 – 10 cm in diameter) to robust (up to 30 or 40 cm in diameter). Leaf scars are prominent and demarcate conspicuous internodes that are mostly green near stem tip (yellowish green, yellow, orange to red purple with stripes in C. renda and its cultivars) and become brown to greyish near the base. The stem in cross section displays an outer cortex consisting of a thin layer of about 4 mm and an inner cortex with vascular bundles. As in Actinorhytis, Ptychococcus or Rhopaloblaste (Banka & Baker 2004) the outer stem is usually very hard while the inner part is softer with sparser fibres. However, wood of Cyrtostachys has a lower number of black fibres and is only used for certain construction purposes. It cannot be used for traditional weapons such as bows, arrow-heads, and spears (Heatubun et al. in prep.).

Leaves

The crown consists of leaves ranging from about 6-7per stem in Cyrtostachys glauca to 14 in C. loriae. There are three types of crown outline in the genus: spherical (C. barbata, C. glauca and C. loriae), hemispherical (C. elegans) and shuttle-cock shaped (C. bakeri, C. excelsa and C. renda). According to Tomlinson (1990) the shuttle-cock or feather duster crown shape results from relatively few leaves in the crown, with the leaf axis held at a high angle and abscission of the leaf taking place as a unit before the axis droops. In contrast, C. glauca has the lowest number of leaves in the genus and has a spherical crown shape. All species of Cyrtostachys have regularly pinnate leaves, except for C. excelsa, in which leaflets are irregularly arranged in 1s or 2s. The inclination of leaflets, whether porrect or pendulous, is associated with the crown outline. Pendulous leaflets occur in spherical and hemispherical crowns and the porrect leaflets in shuttle-cock shaped crowns, except in C. bakeri which has a shuttlecock shaped crown with pendulous leaflets (Fig. 5A), and C. excelsa which has a shuttle-cock shaped crown and slightly curved-porrect leaflets. The thickness and coloration of leaflets when dried are leathery and discolorous in general in Cyrtostachys, except in C. glauca that has papery leaflets, and C. excelsa that has concolorous leaflets. The petiole is almost missing to short (to $10~{\rm cm}$ long) in a few species, and elongate to $50~{\rm cm}$ in $\it C.~renda$ and more than $50~{\rm cm}$ (to $100~{\rm cm}$) in $\it C.~glauca$.

The long tubular leaf sheaths form a well-defined crownshaft. The crownshaft is glaucous only in *Cyrtostachys glauca*. In *C. renda* the crownshaft is bright red to orange, and in other species is green. The leaf sheath is thick and sometimes has disintegrating fibres at the margins just below the petiole.

The leaf anatomy of *Cyrtostachys* is discussed briefly by Tomlinson (1961) based on his observation on *C. lakka* (= *C. renda*), and he noted that *Cyrtostachys* is readily distinguished from other Arecoid palms in having markedly sinuous epidermal cell-walls and having the hypodermal layer made up mostly of fibres instead of colourless cells.

Indumentum

Indumentum in Cyrtostachys occurs on leaf sheaths, leaves and inflorescences. A number of types of indumentum occur on the leaves. Fine purple scales, filamentous brown scales and brown to black thick scales occur on leaf sheaths; thin to thick, caducous, white, scale-like indumentum, with scattered, filamentous, brown to dark brown scales occurs on the petiole; dense white or brown scales occur on the leaf rachis, and inflexed, filamentous brown ramenta occur scattered and/or continuous along the abaxial surface of the mid-veins of the leaflets. The inflorescences carry less indumentum than the leaves, although brown to rusty brown woolly indumentum is present on the rachillae. The presence of beard-like filamentous brown ramenta along the mid-vein on the abaxial leaflet surface is a crucial character in recognising C. barbata from other species (Fig. 6C).

Inflorescence

All Cyrtostachys species have infrafoliar inflorescences and are branched from two to four orders. The 2keeled prophyll encloses the inflorescence until leaf fall, borne just above the winged base of the peduncle and is tubular and lanceolate with winged margins, splitting and soon caducous. The single peduncular bract is similar to the prophyll and it too is soon caducous. Inflorescences are strongly divaricate (Fig. 1) with most basal branches rather diffuse and spreading. The peduncle is usually very short, oval in cross section. First order branches are robust, almost as thick as the main axis (Barfod et al. 2001), spreading, and with a short bare portion at the base, then branching to produce diverging rachillae or second-order branches; second order branches, when not bearing flowers, also have a short bare portion and then branch to produce rachillae. The rachillae are elongate, cylindrical, rather robust, glabrous, papillose, minutely roughened or indumentose, often brightly coloured and expanding long before anthesis. The

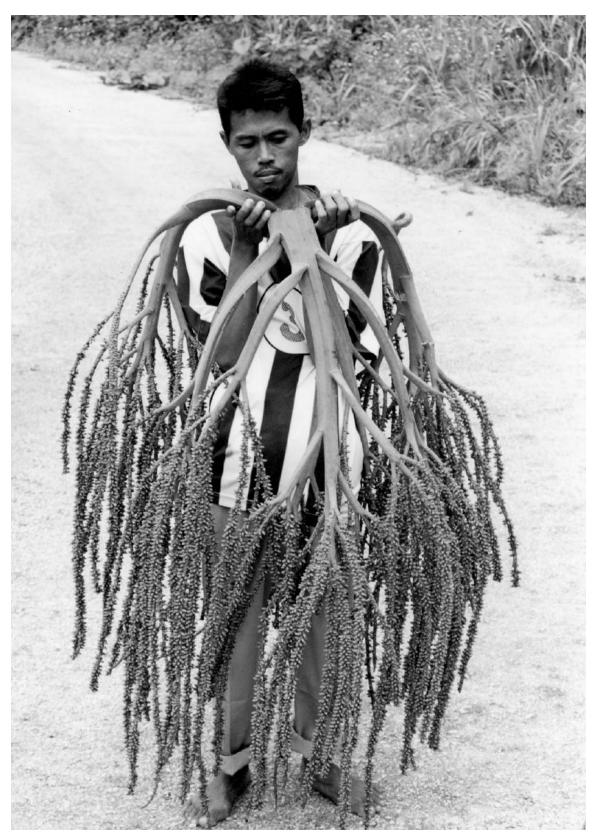


Fig. 1. Cyrtostachys Ioriae Becc. in Japen Island (Heatubun et al. 546) — strongly divaricate inflorescence with young fruits. PHOTO: CHARLIE D. HEATUBUN.

rachilla bracts are low, triangular, spirally arranged, rather crowded, each partially enclosing a shallow pit bearing a triad of flowers.

The numbers of orders of branches of the inflorescence and the nature of pits have important taxonomic value to define species in Cyrtostachys. An inflorescence branched to two orders is only found in C. renda. Four orders of branching are found in C. elegans and C. excelsa, while the other species have inflorescences branched to three orders. There are variations in the abundance and depth of pits from species to species, from superficial pits in C. glauca (Figs. 7D – E) to deep pits in C. loriae (Figs. 8D – E).

Inflorescences in *Cyrtostachys* change in colour as they develop, from cream-coloured at the beginning after the prophyll has fallen, followed by greenish to green at flowering stage (anthesis of male flowers) to fruiting (young fruits), then yellowish-brown to dark brown at ripening (ripe fruits). All species follows this sequence, except *C. excelsa* and *C. renda*. In *C. excelsa*, pink to reddish-purple colour occurs after the prophyll has fallen until the phase before anthesis of male flowers, while *C. renda* has reddish-purple to blackish rachillae at fruiting (young fruits) to ripening stage (ripe fruits).

Flowers

In common with almost all Arecoideae, the flowers are arranged in triads of a central pistillate flower and two lateral staminate flowers, borne in pits along the entire length of the rachilla (e.g. Fig. 7D). The staminate flowers are cream-coloured to greenish-yellow in bud and white to cream-coloured at anthesis. The staminate flowers are about the same size as or slightly smaller than the pistillate. At the beginning of rachilla emergence the pistillate flowers are not visible, being obscured by the staminate buds. Once the staminate flowers have fallen, the pistillate flowers become visible and enlarge.

Staminate flowers have three, distinct, imbricate, broad, strongly keeled sepals with minutely toothed margins; the petals are about twice as long as the sepals, united at the base to about one third their length distally with triangular, valvate tips. Stamens number 8 to 15, with awl-shaped filaments that are connate basally and inflexed apically in bud, the anthers being dorsifixed and latrorse. The connate petals and stamens are distinguishing key characters for separating *Cyrtostachys* from other genera in the Indo-pacific pseudomonomerous Arecoid palm clade.

Pistillate flowers are about the same size as, or slightly larger than, the staminate flowers. Sepals are three, distinct, rounded, imbricate, the margins minutely toothed; petals are also three, distinct, imbricate proximally, asymmetrical, rounded with short triangular valvate tips. There is a very low mem-

branous staminodal ring, bearing short truncate or irregular triangular teeth. The gynoecium is unilocular, ellipsoidal with three short recurved stigmas (e.g. Fig. 8H, J).

Fruits and Seeds

The fruits are small (to 16×6 mm), varying in shape from ellipsoid, ovoid to obovoid with a beak to sickle-shaped, green to black when ripe, and one-seeded. The seeds are small (to $8 \times 5 \times 5$ mm), globose to ellipsoidal, apically attached, with an orbicular hilum, and homogeneous endosperm with basal embryo (e.g. Figs. 7K, 8K). There is no important taxonomic character in the fruits and seeds useful to separate species. The shape and size of fruits and seeds vary greatly within individuals and populations.

Fruit histology of palms has given major insights into palm systematics (Chapin et. al. 2001; Essig 1977, 1982, 1999; Essig & Hernandes 2002; Essig & Young 1979, 1985; Essig et al. 1999, 2001). Variations of fruit pericarp among the representative species of Cyrtostachys have recently been studied in detail by Fred Essig and co-workers. The genus can be characterised by a combination of a papillate epidermis, a heavy layer of tanniniferous/pigmented cells below the epidermis, a system of vascular bundles with thick fibrous sheaths with purely fibrous bundles frequently above and below, the absence of brachysclereids, and a very thin sclerified locular epidermis (Essig & Litten 2004). The authors found that one species, C. kisu (= C. loriae), appears to be the most distinctive, with relatively few, large bundles and tanniniferous tissue throughout the pericarp.

Pollen Morphology

Pollen morphology was observed using both light microscopy (LM) and scanning electron microscopy (SEM) (Figs. 2 – 3). Using SEM the following details were obtained: the tectum surface (topology) is perforate, rugulate or in some species, verrucate and/or gemmate. Sometimes, in LM or SEM preparations, a few still intact tetrahedral post meiotic tetrads were observed. Pollen morphology for individual species is included in the species descriptions.

Results from pollen morphological data provide limited variation in characters to aid species delimitation, especially in the Papuasian taxa. This reflects the findings of Harley (1999), who conducted a general survey of pollen morphology throughout the genera of the palm family and found that pollen data are not often useful in helping to support delimitation at the species level. However, the data give a clear distinction between the west Malesian *Cyrtostachys renda* and the Papuasian taxa, in which the topology of the tectum surface of *C. renda* is microfossulate-rugulate (Fig. 3J – M), in contrast to the verrucate-gemmate tectum topology in the Papuasian

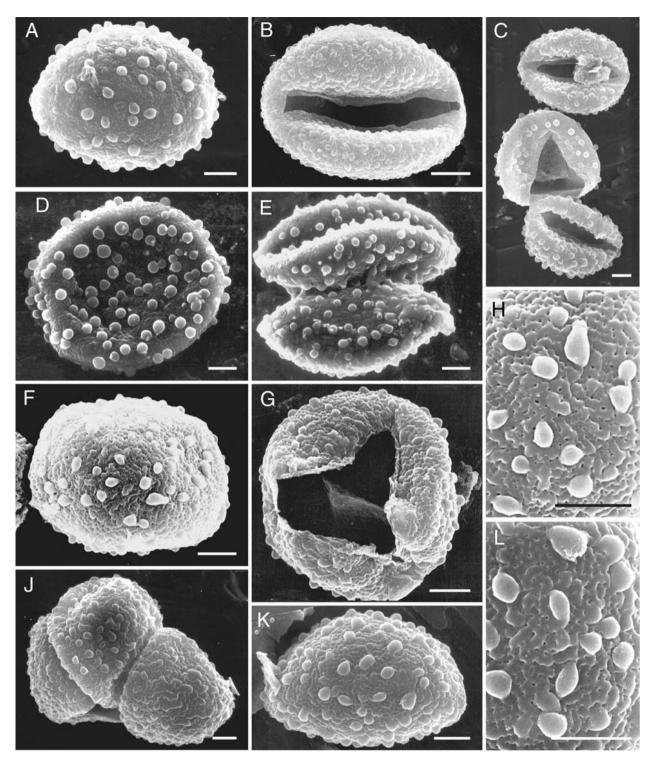


Fig. 2. Some of the pollen morphological diversity in *Cyrtostachys*. A – C *C. bakeri* (from *Baker* 1138): A whole grain, proximal face; B whole grain, distal face; C group of grains to show general appearance of pollen. D, E *C. barbata* (from *Brass* 13707): D whole grain, proximal face; E two rather collapsed grains, apparently conjoined. F – H *C. elegans* (from *Heatubun* 341): F whole grain, proximal face; G whole grain, distal face showing trichotomosulcate aperture; H close up of verrucate surface, proximal face. J – L *C. excelsa* (from *Heatubun* 330): J three grains adhered, showing proximal faces; K whole grain, proximal face; L close up of verrucate surface, proximal face. Scale bar: 5 μm.

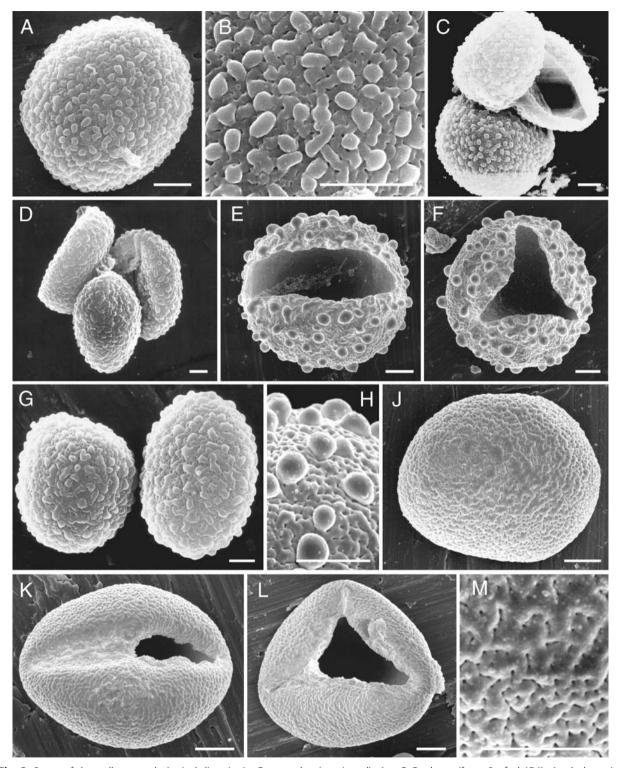


Fig. 3. Some of the pollen morphological diversity in *Cyrtostachys* (continued). A – C *C. glauca* (from *Barfod* 454): A whole grain, proximal face; B close up of verrucate surface, proximal face; C group of grains to show general appearance of pollen. D – H *C. loriae* (D, G from *Barfod* 463; E, F, H from *Whitmore* 3945): D group of grains; E whole grain, distal face showing monosulcate aperture; F whole grain, distal face showing trichotomosulcate aperture; G two grains, showing proximal faces; H close up of gemmate surface, proximal face. J – M *C. renda* (from *Keith* 2491): J whole grain, proximal face; K whole grain, distal face showing monosulcate aperture with membrane semi intact; L whole grain, distal face showing trichotomosulcate aperture; M close up of micro-fossulate surface, proximal face. Scale bar: 5 μm.

species (Figs. 2A - K, 3A - H). As well as Cyrtostachys, these types of tectum surface topology are also found in some species of other palm genera; perforate and rugulate types are the second most widespread ectexine type in the palms and it occurs in all subfamilies except Nypoideae. The tectate verrucate type is uncommon except in Calamus (Calamoideae: Calameae) where it is noted in about seventeen species; in Coryphoideae it is known in Hyphaene (Borasseae: Hyphaeninae) and in Arecoideae there are three other genera where some species have a verrucate, or regulate-verrucate pollen surface — Chamaedorea carchensis Standl. & Steverm. (Chamaedoreeae), Aiphanes (Cocoseae: Bactridinae) and Prestoea (Euterpeae). The gemmate type is one of three ectexine types that have supratectate and intectate forms, supratectate gemmae occur on the ectexine of five species of Calamus (Calamoideae: Calameae), Hyphaene (Borasseae: Hyphaeninae), Borassus (Borasseae: Lataniinae), Attalea (Cocoseae: Attaleinae), Bactris (Cocoseae: Bactridinae), Ceroxylon (Ceroxyloideae: Ceroxyleae), Dictyocaryum and Iriartea (both Arecoideae: Iriarteeae) and Voanioala (Cocoseae: Attaleinae).

Phylogenetic Analysis

The cladistic analysis of morphological and palynological data generated eight equally most parsimonious trees (length=26 steps, consistency index=0.69, retention index=0.79, rescaled consistency index=0.55). A strict consensus of the trees, including bootstrap support values, and a single tree selected randomly from the most parsimonious trees, are shown in Fig. 4.

The topology of the strict consensus tree is poorly resolved and supported (Fig. 4); only three nodes show bootstrap supports above 75%. Although the resolution is low, the monophyly of *Cyrtostachys* is well supported (bootstrap=98%) and *C. glauca* is sister to all remaining species of *Cyrtostachys* (bootstrap=75%). The topology of the tree suggests that *C. renda* dispersed from within New Guinea/Solomon (Papuasia) clade into the Sunda Shelf.

The low resolution of the strict consensus tree gives clear indication of the high level of character conflict caused by homoplasious characters. The recovery of *Cyrtostachys* as a monophyletic genus confirms again its circumscription as a distinct genus. Several uncontradicted synapomorphies optimise at the highly supported node (95% bootstrap support) at the base of the genus: pistillate calyx persistent on rachilla, petals in male flowers connate, filaments in male flowers connate, endosperm homogeneous. The character states "pistillate calyx persistent on rachilla" and "endosperm homogeneous" are also found in other genera of Arecoid palms, but not in outgroups used in this study. Uhl & Dransfield (1987) define *Cyrtostachys* as a genus separate from

other genera by the characters "connate petals and filaments in staminate flowers," also "strongly divaricate inflorescence" and "flowers borne in pits along the rachilla." However, in this analysis these character states are homoplasious because they are also found in one of the outgroups (*Rhopaloblaste ledermanniana* Becc.).

The support of *Cyrtostachys glauca* as sister to all species of *Cyrtostachys* is also predicted; occasionally there has been some doubt as to whether *C. glauca* is a member of the genus *Cyrtostachys* because of the nature of the pits along the rachillae. Other autapomorphic characters (leaf sheath surface glaucous and trichotomosulcate grains absent) also contributed to the isolation of *C. glauca* from other species.

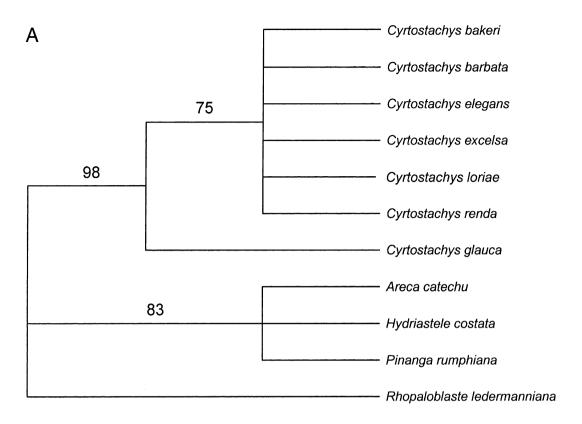
Biogeography and Ecology

Cyrtostachys is a tropical genus with a disjunct distribution pattern; one species (*C. renda*) occurs to the west of Wallace's line from south Thailand to the Malay Peninsula, Sumatra and Borneo, and the other six species on the island of New Guinea to the Solomon Islands. How this disjunct distribution arose has been discussed for three decades (Moore 1973; Dransfield 1981, 1987; Baker *et al.* 1998).

The cladistic analysis suggests that *Cyrtostachys renda* dispersed from within the New Guinea-Solomon (Papuasia) clade into the Sunda Shelf, although there is no evidence yet of macro fossils and/or fossil pollen of *Cyrtostachys* from areas between the two distribution regions of the genus (Van der Kaars, pers. comm.) to support that analysis. In fact, information generally from macro fossils and fossil pollen in the Indonesia archipelago is rather poor, especially in the gap between the two distribution regions of *Cyrtostachys*. Four locations of excavation have been reported so far, they are: Banda Sea (Van der Kaars *et al.* 2000), Halmahera and North Moluccas Sea (Barmawidjaya *et al.* 1993), and Tondano (Dam *et al.* 2001). Further study is needed.

Meanwhile, New Guinea appears to be the centre of diversity for *Cyrtostachys*, based on numbers of species. Six of the seven species of *Cyrtostachys* currently recognised in this monograph are originally from New Guinea. The complex and rapid tectonic change as well as climate and the wide range of ecological conditions are probably the major causes of speciation in New Guinea (Pigram & Davies 1987; Van Welzen 1997; Bachman *et al.* 2004).

Cyrtostachys occurs in a wide range of ecological conditions from swampy areas in lowlands to heath forest in lower montane vegetation, from evergreen rain forest to dry areas in savannah lands and from the continental to small off-shore islands, with *C. renda* and *C. loriae* widespread species in each region in west Malesia and Papuasia respectively.



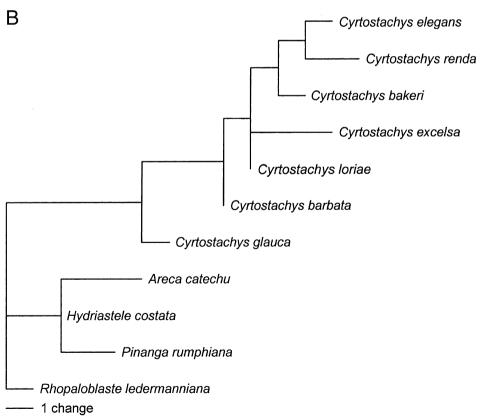


Fig. 4. A Strict consensus of 8 most parsimonious trees found from cladistic analysis of morphological and palynological data from *Cyrtostachys*. Numbers above branches indicate bootstrap support. **B** One of 8 most parsimonious trees (length = 26 steps, CI = 0.69, RI = 0.79, RCI = 0.55) found from cladistic analysis of morphological and palynological data from the genus *Cyrtostachys*.

Uses

Ethnobotanical information on Cyrtostachys, especially of the New Guinean taxa, will be discussed in detail by Heatubun et al. (in prep.), but in general the genus Cyrtostachys plays an important role in the traditional life of local communities. Many parts of the palm are utilised: the stem, leaves, leaf sheath, cabbage (palm heart), and mid-vein of leaflets. The species C. loriae in particular, has been widely used by indigenous people in New Guinea through to the Solomon Islands for construction materials in traditional house (piling, flooring, thatching), and bridge building, as water pipes and in other local methods of construction, such as tools, weapons and other equipment including mattresses. The remarkable species C. renda has been established in horticulture as an ornamental and has substantial economic importance. Many botanic gardens and palm collectors all over the world put this species as a priority in their collection lists. A number of cultivars have been described from cultivation (Tucker 1992; Ellison & Ellison 2001; Waddel 2002).

In addition, the local names, common names, trade names, and folklore or mythologies that we found for the genus *Cyrtostachys* give proof of the relationship between species of *Cyrtostachys* and the human communities living near the habitat of this palm.

Taxonomic Treatment

Cyrtostachys *Blume* (1838: 66; 1843: 101); Moore (1973: 107); Dransfield & Uhl (1986: 8); Uhl & Dransfield (1987: 378). Type: *C. renda* Blume.

Solitary or clustering, moderate to robust, unarmed, pleonanthic, monoecious palms. Stem erect, bare, conspicuously ringed with leaf scars, often bearing a mass of adventitious roots at the base, where clustering, the clump rather close, or more diffusely spreading by stolons. Leaves pinnate, neatly abscising; sheath tubular, forming a well defined crownshaft, brilliantly orange-red coloured in one species (C. renda), glabrous or scaly; rachis like the petiole but angled adaxially; leaflets always single-fold, acute or acuminate or sometimes rounded with a bifid tip, regularly arranged or grouped with two leaflets in one species (C. excelsa), often stiff, sometimes slightly paler beneath, ± glabrous adaxially, abaxially often with ramenta along mid vein and sometimes minutely dotted between the veins, transverse veinlets conspicuous or obscure. Inflorescence apparently protandrous, infrafoliar, branched to 2 - 4 orders, rather diffuse and spreading; peduncle usually very short, ± oval in cross section; prophyll enclosing the inflorescence until leaf fall, borne just above the winged base of peduncle, tubular, 2-keeled, ± lanceolate, with

winged margins, splitting, soon caducous; peduncular bract borne just above the prophyll, completely enclosing the inflorescence, splitting longitudinally like the prophyll, caducous; subsequent bract very inconspicuous, incomplete, low, triangular; rachis longer than the peduncle; first order branches robust, spreading, with a short bare portion at the base, then branching to produce diverging rachillae or secondorder branches; second-order branches, when not rachillae, also with short bare portion and then branching to produce rachillae; rachillae elongate, cylindrical, rather robust, glabrous, papillate, minutely roughened or indumentose, sometimes brightly coloured, expanding long before anthesis; rachilla bracts low, triangular, spirally arranged, rather crowded, each partially enclosing a shallow pit bearing a triad of flowers, triads borne throughout the length of the rachillae; floral bracteoles membranous, very small and inconspicuous. Staminate flowers with 3, distinct, imbricate, broad, strongly keeled sepals with minutely toothed margins; petals about twice as long as sepals, united at the base to c. 1/3 their length, distally with triangular, valvate tips; stamens 8 - 15, the filaments awl-shaped, connate basally, apically inflexed in bud, anthers dorsifixed, latrorse; pollen grains ellipsoidal, less frequently, oblate triangular, symmetric or slightly asymmetric; aperture a distal sulcus or trichotomosulcus; ectexine tectate, perforate, rugulate, in some species with verrucate or gemmate supratectal processes, aperture margin similar; infratectum columellate; longest axis ranging from 27 – 57 μm, shortest axis ranging from 23 - 44 µm; post-meiotic tetrads tetrahedral; pistillode almost as long as filament, narrow, elongate, trifid. Pistillate flowers about same size as or slightly larger than the staminate; sepals 3, distinct, rounded, imbricate, the margins minutely toothed; petals 3, slightly larger than sepals, distinct, imbricate, proximally asymmetrical, rounded with short triangular valvate tips; staminodal ring membranous, very low, bearing short truncate or irregularly triangular teeth; gynoecium unilocular, ellipsoidal with 3 short recurved stigmas, ovule pendulous from apex of locule, form unknown. Fruits 1-seeded, broad to narrow-ellipsoidal or sickle-shaped, usually black, the perianth whorls persistent, stigmatic remains apical; epicarp smooth, contrasting with rachilla, mesocarp thin, closely adhering to the seed; pericarp anatomy: combination of papillate epidermis, heavy layer of tanniniferous/pigmented cells below the epidermis, a system of vascular bundles with thick fibrous sheaths with purely fibrous bundles frequently above and below, absence of brachysclereids, and a very thin sclerified locular epidermis. Seed globose or ellipsoidal, apically attached, the hilum orbicular, endosperm homogenous; embryo basal. Germination adjacent-ligular; eophyll bifid with narrow lobes. Cytology n = 16 (*C. renda*, Sarkar 1970).

Key to Species of Cyrtostachys

	, , , , ,	
1.	Crownshaft and leaf sheath orange to bright red; West Malesia (Southern Thailand, Malay Peninsula, Sumatra	a,
	Borneo)	la
	Crownshaft and leaf sheath glaucous and green; Papuasia (New Guinea to the Solomon Islands	2
2.	Crownshaft and leaf sheath glaucous; elongate petiole (25 – 100 cm long); inflorescence slender, whitish whe	'n
	dried, and rachilla with superficial pits	ca
	Crownshaft and leaf sheath green; petiole relatively short (less than 20 cm long); inflorescence relatively large	
	to robust, not whitish when dried, and rachilla with deep pits	3
3.	Leaflets irregularly arranged	
	Leaflets regularly arranged	
4.	Leaflets pectinate with beard-like ramenta continuous along mid-vein on abaxial surface of leaflets	
	Leaflets regularly pinnate, ramenta rare on abaxial surface of leaflets	
5.	Stem solitary; crown spherical in outline	
	Stem clustered; crown not spherical in outline	
6.	Crown shuttle-cock shaped in outline; inflorescence compact, branched to 3 orders; stamens 12 1. C. bake	
	Crown hemispherical in outline; inflorescence elongate, branched to 4 orders; stamens 9 3. C. elegar	

Species Accounts

1. Cyrtostachys bakeri *Heatubun* sp. nov. palma montana elata caespitosa 3 truncis, corona 8 foliis porrectis, petiolo breve, 4 – 10 cm longo, foliolis pendulis, crassis coriaceis, in sicco supra griseo-brunneis, infra palidioribus, inflorescentia in 3 ordines ramificanti, staminibus 12, pistillodio 3 lobis teretis membranaceis, distincta. Typus: Papua New Guinea, Western Province, North Fly Distr., Junction of Harvey Creek and Ok Mani R., 10 km WNW of Tabubil, Dec. 2000, *Baker et al.*1138 (holotypus K!; isotypi AAU, LAE, NY).

Robust, clustering tree palm 15 - 25 m, with up to 3 - 7adult stems. Stem 15 - 25 cm in diam.; internodes 10 -20 cm long; crown appearing shuttle-cock shaped. Leaves 8 in crown, almost erect, with pendulous leaflets, 400 - 450 cm long (including petiole); sheath tubular, 110 - 130 × 40 cm; crownshaft c. 180 cm long, 15 -25 cm in diam., whitish to mid-green with numerous fine purple scales; petiole 4 – 10 cm long, c. 4 cm wide and 2 cm thick at the base, channelled adaxially, rounded abaxially; leaflets regularly arranged, leathery, 78-90 leaflets on each side, middle leaflets c. $92 \times$ 5 cm, apical leaflets c. 30×1.5 cm, briefly pointed and sometimes notched at apices, green, discolorous when dried, brown adaxially, paler abaxially, with fine sparse ramenta on mid-vein on abaxial surface. Inflorescence infrafoliar, strongly divaricate, 90 - 120 cm long, branched to 3 orders, c. 15 primary branches, proximal pair strongly recurving; prophyll and bract caducous, not seen; peduncle c. 16 cm, caducous, not seen; rachillae c. 55 - 57 cm long and c. 9 mm diam., rachilla bract conspicuous, low, calyx persistent on rachillae after fruits fallen; 20 - 22 pits in 1 cm of rachilla length (at fruiting stage), pits 2 mm in diam. Staminate flowers c. 2.3×2.3 mm, asymmetrical; sepals c. 2×2 mm, imbricate, rounded, strongly keeled; petals c. 2 ×

1.75 mm, triangular, brown in apical and basal parts; stamens 12; filaments c. 1×0.1 mm; anthers $1-1.1 \times 0.5-0.7$ mm; pollen size, long axis 34-45 µm, short axis 35-40 µm, proximal wall thickness 2-3 µm, distal wall thickness 2-3 µm, tectum surface verrucate, trichotomosulcate grains present; pistillode 0.8×0.3 mm, trifid, separated almost to the base, membranous. *Pistillate flowers* c. 3×2.8 mm; sepals $2-3 \times 2-2.5$ mm, imbricate, strongly keeled and dark brown to black; petals $2-2.3 \times 1.5-2$ mm; gynoecium 1.8×0.8 mm (including stigma 0.5 mm); staminodes circular, membranous. *Fruits* $9-25 \times 3-5$ mm, elongated, pointed tips, hard, black when ripe. *Seeds* $7-8 \times 4-4.5$ mm, ovoid, rounded apically and flattened basally, hard; endosperm homogenous. (Figs. 2A-C, 5).

DISTRIBUTION. Known only from the type collection from Tabubil area in North Fly Distr., Western Province in Papua New Guinea and one collection in cultivation in Lae Botanic Garden.

SPECIMENS EXAMINED. PAPUA NEW GUINEA. Western Province, North Fly Distr., Junction of Harvey Creek and Ok Mani R., 10 km WNW of Tabubil, c. 750 m a.s.l., Dec. 2000, *Baker et al.* 1138 (holotype K!; isotypes AAU, LAE, NY). CULTIVATED. Lae Botanic Garden, main palm collection, Nov. 2006, *Baker & Fazang* 1308 (K, LAE, MAN).

HABITAT. Growing in the forest on valley side near the river margin at an altitude of c. 750 m above sea level. **VERNACULAR NAME.** Not known.

USES. Not known.

CONSERVATION STATUS. Data Deficient (DD). The conservation status of this palm is not known. The information about this species is based on just one collection from the vicinity of Tabubil area, Papua New Guinea. More population and distribution data are required.

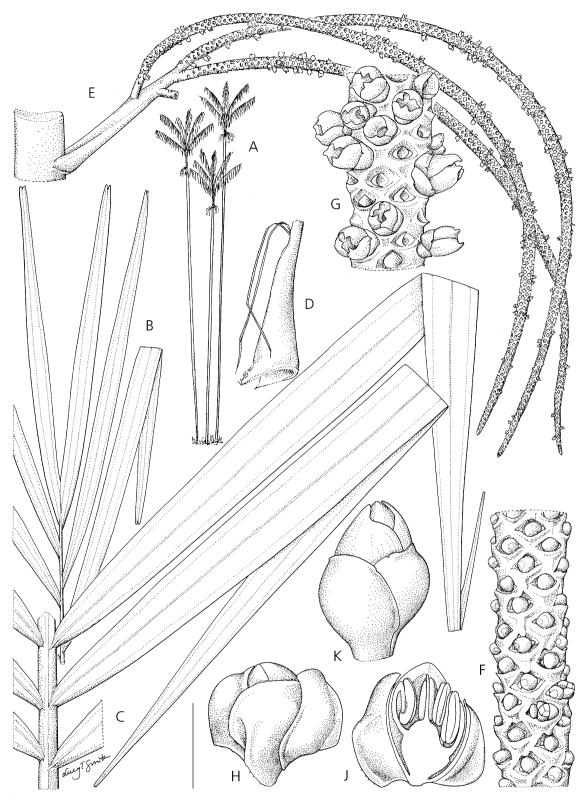


Fig. 5. *Cyrtostachys bakeri.* A habit; B apical portion of leaf; C middle portion of leaf; D leaf sheath, upper part; E portion of inflorescence; F detail of rachilla; G portion of rachilla with perianth of pistillate flowers persisting; H, J staminate flower whole and in section; K pistillate flower. Scale bar: A = 5 m; B, C = 8 cm; D = 20 cm; E = 6 cm; F, G = 1 cm; H, J = 1.6 mm; K = 3 mm. All from *Baker* 1138. DRAWN BY LUCY T. SMITH.

NOTES. Cyrtostachys bakeri differs from all other species in its leathery leaflets that are relatively widely spaced, in its pits being the most congested in the genus with 20-22 pits in a 1 cm length of rachilla, and in its membranous pistillode with lobes separate to the base. It is also the only species that possesses both a shuttle-cock shaped crown and pendulous leaflets. It is most similar to *C. elegans* in the robust, clustering habit and pendulous leaflets, but differs in the shuttle-cock-shaped crown, the inflorescence branched to 3 orders, the 12 stamens and the habitat at relatively high elevation (c. 750 m a.s.l.).

Cyrtostachys bakeri is named for the collector of the specimen, Dr William J. Baker, palm botanist and head of the palm section of the Royal Botanic Gardens, Kew, UK, in recognition of his contributions to palm botany as a whole and in New Guinea, in particular.

2. Cyrtostachys barbata *Heatubun* sp. nov. palma solitaria montana, habitu *C. loriae* Becc. similis, sed petiolo 16 – 20 cm longo, petiolo rachideque indumento pallido vel brunneo dense tecto, foliolis confertis, crassis, in sicco supra glaucis vel brunneis, infra griseis, infra secus costam ramentis brunneis dense tectis, inflorescentia parva rachillis gracilibus foveis vadosis ferentibus, staminibus 8 – 10, differt. Typus: Indonesia, Papua Province, Sarmi distr., Mamberamo, Idenburg R., 4 km of SW Bernard Camp, 900 m a.s.l., March 1939, *Brass* 13707 (holotypus L!; isotypi A!, BO!)

Large, solitary tree palm to 25 m. Stem 13 - 20 cm in diam., glossy green apically and brown basally, nodal scars very conspicuous. Leaves c. 348 cm long (including petiole); sheath tubular, c. 143 cm long, c. 38 cm diam., fibrous at margin near petiole, forming distinct crownshaft, green; petiole 16 - 20 cm long, 4 - 5 cm wide and 1.5 - 2 cm thick at the base, covered in thick white indumentum, and scattered filamentous, brown scales; leaflets regularly arranged, pectinate, leathery, number of leaflets on each side not known, middle leaflets c. 105.5×6.5 cm, apical leaflets c. 23×2.5 cm, briefly pointed with long tip and sometimes rounded and notched at apices, green, discolourous when dried, light brown to glaucous adaxially, paler brown to whitish abaxially, with thick, membranous brown ramenta, inflexed, beard-like and continuous along mid-vein abaxially. Inflorescence slender, branched to 3 orders, light brown to whitish brown when dried; rachilla 43 - 49 cm long; c. 4 mm diam.; pits superficial to shallow, 13 pits in 1 cm length rachilla (at fruiting stage), pit 2 – 3 mm diam. Staminate flowers c. 3.5×2.6 mm; sepals $1.5 - 2 \times$ 2 mm; petals c. 2.5×1.8 mm; stamens 8 - 10; filaments $2.5 \times 0.2 - 0.5$ mm; anthers $1 - 1.1 \times 0.5 - 0.8$ mm; pollen size long axis $38 - 53 \mu m$, short axis $24 - 35 \mu m$, proximal wall thickness $3-4~\mu m$, distal wall thickness 1-3 µm, tectum surface gemmate, trichotomosulcate grains present; pistillode $1.5 \times 0.5 - 0.8$ mm. Pistillate flowers c. 3×3.3 mm; sepals $2.5 - 2.7 \times 2.5 - 3$ mm; petals $3.5 - 4 \times 3 - 4$ mm; gynoecium c. 2.8×1.2 mm (including stigma). Fruits c. 12×5 mm, ellipsoid to sickle-shaped; beak 2 mm long. Seeds c. $5 \times 4 \times 4$ mm, ovoid, rounded apical and flatted basally. (Figs. 2D - E, 6).

DISTRIBUTION. This palm is known only from its type locality in the Idenburg R. area, Mamberamo basin, Indonesian Province of Papua.

SPECIMEN EXAMINED. INDONESIA. Papua Province. Sarmi distr.; Mamberamo, Idenburg R., 4 km of SW Bernard Camp, 900 m a.s.l., March 1939, *Brass* 13707 (holotype L!; isotypes A!, BO!)

HABITAT. Growing in primary forest on slopes in *Agathis* forest at an altitude of 900 m above sea level. **VERNACULAR NAME.** *Nibung* (Indonesian dialect in Papua, also used for other tree palms).

USES. Not known.

CONSERVATION STATUS. Data Deficient (DD). Cyrtostachys barbata is only known from one collection made by L. J. Brass in Mamberamo basin, Indonesian Province of Papua, although in Brass's field notes he noted that the palm was common in Agathis forest and rain forest on slopes. Agathis is an important timber tree in New Guinea and provides a luxury wood for the timber trade, so the extensive logging activities in that area will very likely affect the entire population of this palm. More populations and distribution data are required to assess the conservation status of this species. **NOTES.** Cyrtostachys barbata is similar to C. loriae in habit. but differs from the latter and other species in the presence of continuous beard-like brown ramenta along the mid-veins on the abaxial surface of leaflets, the very short space between leaflets giving the leaf a pectinate appearance, rachis and petiole covered by thick white indumentum and scattered filamentous brown scales; the slender rachillae with congested superficial pits and the habitat in Agathis forest at high altitude (900 m a.s.l.).

Cyrtostachys barbata also differs from *C. elegans* in its solitary habit, the elongate petiole and inflorescences branched to three orders, rather than clustering habit, short petiole and inflorescence branched to four orders. It also differs from *C. glauca* in its solitary habit and hemispherical crown outline, rather than clustering habit and spherical crown.

Unlike other species in the genus, *Cyrtostachys barbata* and *C. glauca* have slender rachillae with superficial to shallow pits, but *C. barbata* has brown rachillae when dried and congested pits c. 13 per 1 cm rachilla length, while *C. glauca* has white rachillae when dried and sparse pits 3 – 5 per 1 cm rachilla length.

The specific epithet came from Latin word *barbatus* meaning bearded, in reference to the dense ramenta along the mid-vein that contrast with the white colour of the abaxial leaflet surface. This specimen was seen

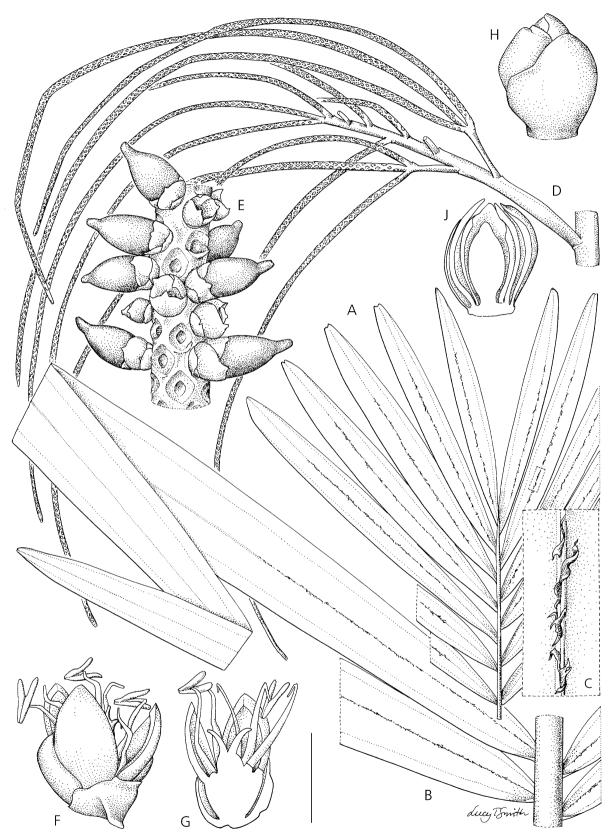


Fig. 6. *Cyrtostachys barbata*. A apical portion of leaf; B middle portion of leaf; C detail of ramenta; D portion of inflorescence; E portion of rachilla in fruit; F, G staminate flower whole and in section; H, J pistillate flower whole and in section. Scale bar: A, B = 8 cm; C = 5 mm, D = 6 cm; E = 1 cm; F – J = 2.5 mm. All from *Brass* 13707. DRAWN BY LUCY T. SMITH.

by H. E. Moore in 1956 and identified as Cyrtostachys ledermanniana Becc. with a question mark behind that name. A few characters of C. barbata, especially regarding leaf and rachilla, fit with C. ledermanniana based on Beccari's description in the protologue (Beccari 1923). However, C. ledermanniana was described from very inadequate material; Beccari made his description based on two different Ledermann collections (Ledermann 9063 and 7175). These specimens came from two different areas in Papua New Guinea. Ledermann 9063 was collected from Ettapenberg at 850 m a.s.l., and from this specimen, Beccari made a brief description of habit, leaves, inflorescence, flowers, fruits and seeds. He wrote his description of the staminate flowers from Ledermann 7175 from the Sepik area in the swamp forest at an altitude 20 -40 m a.s.l. The type of C. ledermanniana, and almost all the Ledermann's collections were destroyed during the Second World War in Berlin, and we have been unable to locate another duplicate. Thus, C. ledermanniana is treated as an imperfectly known taxon in this monograph.

3. Cyrtostachys elegans *Burret* (1937: 472). Type: Cultivated in Bogor Botanic Garden, II.F. 17. ex New Guinea, April – May 1936, *Furtado* SFN 3/1/28 (holotype B†; isotype K!, L!, SING).

Robust, clustering tree palm to 15 (-20) m, with up to c. 3 adult stems and 4-6 or more suckers at the base. crown hemispherical in outline. Stem 15 - 30 cm diam., greyish green apically, greyish brown to black near base; internodes c. 25 cm long. Leaves 9 in crown, curved, 300 - 350 cm long (including petiole); sheath tubular, c. 33 cm wide, forming a distinct crownshaft, c. 250 cm long, light green to pale yellow; petiole short to 10 cm long, 3.5 - 4 cm wide and 1.5 - 2.5 cm thick at the base, channelled adaxially, rounded abaxially; leaflets pendulous, regularly arranged, leathery, 100 - 102 leaflets on each side, middle leaflets $100 - 126.5 \times 3.5 - 4.5$ cm, apical leaflets c. 33.5 × 1 cm, briefly pointed and sometimes notched at apices, green, discolorous when dried, light brown adaxially, pale brown to whitish abaxially, fine brown ramenta discontinuous along midvein on abaxial surface. Inflorescence 75 – 100 cm long, c. 160 cm wide, branched to 4 orders, creamy to yellowish green, brown when dried; prophyll c. 65 × 24 cm, leathery, peduncular bract similar to prophyll; peduncle very short to 7.5 cm; rachillae 34 – 61.5 cm long; 17 – 19 pits per 1 cm rachilla length (at fruiting stage), pits 2-4 mm diam. Staminate flowers $2-2.5 \times 2-$ 2.7 mm, asymmetrical; sepals $1.8 - 2.3 \times 1.5 - 2$ mm; petals $1.4 - 2 \times 1.3 - 1.5$ mm; stamens 9; filaments 0.5 - $1.5 \times 0.1 - 0.3$ mm; anthers $0.5 - 1 \times 0.3 - 0.7$ mm; pollen size long axis $31 - 42 \mu m$, short axis $24 - 42 \mu m$, proximal wall thickness 1 - 3 µm, distal wall thickness 1-2 μm, tectum surface verrucate, less frequently gemmate, trichotomosulcate grains present; pistillode $0.8-1.3\times0.3-0.5$ mm, trifid. *Pistillate flowers* $2-5.2\times1.3-4.5$ mm; sepals $1.6-4.8\times1-3.5$ mm; petals $1.2-3.8\times0.5-3.9$ mm; gynoecium $0.9-4.5\times0.4-2.5$ mm (including stigma); staminodes 4-5, membranous. *Fruits* $12-17\times5-6$ mm, ellipsoid to sickle-shaped, green to black (when mature); beak 1-2 mm long, perianth persistent, forming a narrow cylinder at the base or leaving a different coloured scar, $\frac{1}{3}-\frac{1}{2}$ length of fruit. *Seeds* $6-7\times4-5\times4$ mm, ellipsoid, rounded apical and flatted basally. (Fig. 2F-H).

DISTRIBUTION. Cyrtostachys elegans is a Central-West New Guinean species and is known only from lowlands in Nabire and Timika in the Indonesian Province of Papua.

SPECIMENS EXAMINED. INDONESIA. Papua Province, Nabire distr.; Wanggar, Bumi R., Satuan Pemukiman Transmigrasi C (SP-C), c. 10 m a.s.l., Feb. 2001, Heatubun et al. 341 (K!, AAU!, MAN!); Bivak Kanehira, 10 km inward from mouth of Bumi R., c. 100 m a.s.l., March 1940, Kanehira & Hatusima 12851 (A!); Bumi R., 40 km inward of Nabire, c. 300 m a.s.l., March 1940, Kanehira & Hatusima 12747 (A!). Mimika distr., Timika area, PT. Freeport Indonesia Concession area, East levee by drowned forest, 5 km S of Kampung Kali Kopi, alt. 20 m a.s.l., Feb. 1998, Heatubun et al. 194 (AAU!, BH!, BO!, K!, L!, MAN!). CULTIVATED. Bogor Botanic Garden origin from New Guinea, II.F.17, May 1936. Furtado SFN 3/1/28 (K!, L!, SING isotypes): XII. E.40, April – May 1936, Furtado SFN 3/1/06 (K!, L!, SING).

HABITAT. This palm grows in swampy areas in lowland rain forest at an altitude 10 - 300 m above sea level. **VERNACULAR NAME.** *Nibung* (Indonesian dialect in Papua, also used for other tree palms).

USES. Not known.

CONSERVATION STATUS. Near Threatened (NT). The resettlement and relocation of Nabire town after being hit by a large earthquake recently, and the development in the Timika area to support PT. Freeport Indonesia (the world biggest copper and gold mining company) mining activities will affect the population of this palm. Large areas of forest in the lowlands will disappear.

NOTES. Cyrtostachys elegans is similar to C. loriae in being a robust tree palm with pendulous leaflets and short petiole, but differs from the latter in its clustering habit, the hemispherical crown and elongate inflorescence branched to 4 orders, rather than solitary habit, spherical crown and robust inflorescence branched to 3 orders. This species also differs from the other New Guinean robust tree palm C. bakeri in the presence of curved leaves and hemispherical crown, rather than erect leaves and shuttle-cock crown; however, both species have pendulous leaflets.

This species was described by Burret in 1937 based on a herbarium specimen made by C. X. Furtado from a plant cultivated in the Bogor Botanical Garden.

4. Cyrtostachys excelsa *Heatubun* **sp. nov.** palma solitaria calciphila, corona 7 foliis erectis rigidisque, petiolo breve, 11 – 15 cm longo, foliolis irregulariter binatim dispositis, crassis coriaceis, in sicco supra atrobrunneis, infra palidioribus, inflorescentia in 4 ordines ramificanti, rosea vel purpurea, staminibus 12 differt. Typus: Indonesia, Papua Province, Nabire distr., Kwatisore, Pintu Angin, km-14 road of PT. Kaltim Hutama, Feb. 2001, *Heatubun et al.* 330 (holotypus K!; isotypi AAU!, MAN!).

Robust, solitary tree palm to 25 m. Stem c. 15 cm diam., greyish to white in colour, nodal scars conspicuous; internodes c. 30 cm long, crown appearing shuttle-cockshaped in outline. Leaves c. 7 in crown, stiff, slightly recurved, 250 – 300 cm long (including petiole); sheath tubular, c. 30 cm wide, forming a distinct crownshaft; petiole 11 – 15 cm long, c. 4 cm wide and 2 cm thick at the base, channelled adaxially, rounded abaxially, with thin, caducous, dark brown indumentum; leaflets irregularly arranged in 1s or 2s, leathery, c. 80 leaflets on each side, middle leaflets c. 112 × 4 cm, apical leaflets c. 28.5×1.7 cm, briefly pointed and sometimes notched at apices, green, concolorous when dried, light to chocolate-brown on both surfaces; rachis with thin, caducous, fine lepidote indumentum, interspersed with white scales. Inflorescence infrafoliar, strongly divaricate, c. 100 cm long, branched to 4 orders, pink to reddishpurple when young to greenish-grey when mature and dark brown when dried; peduncle very short; rachilla 50 - 75 cm long; c. 15 pits per 1 cm rachilla length (before anthesis). Staminate flowers 2.5 × 2.5 mm, asymmetrical; sepals c. 2.1×2 mm, imbricate, rounded, strongly keeled; petals c. 1.9 x 1.8 mm, striate, triangular; stamens 12; filaments 1×0.1 mm; anthers $1 \times 0.5 - 0.6$ mm; pollen size: long axis 35 - 42 µm, short axis 33 - 42 µm, proximal and distal wall thickness 2 - 3 µm, tectum surface verrucate, less frequently gemmate, trichotomosulcate grains present; pistillode 1×0.3 mm, trifid. Pistillate flowers c. $3.1 \times$ 2.5 mm; sepals c. 2.2 × 2 mm, imbricate, strongly keeled, dark brown to black; petals c. 2.5 × 1.5 mm, triangular; gynoecium 1.8 × 0.5 mm (including stigma 0.7 mm); staminodes 3, triangular, membranous. Fruits not seen. Seeds not seen. (Fig. 2J - L).

DISTRIBUTION. Only known from one locality in forest on slopes at Pintu Angin (14 km on the road of the logging company PT. Kaltim Hutama) near Kwatisore village, Nabire distr., Papua.

SPECIMEN EXAMINED. INDONESIA. Papua Province. Nabire distr.; Kwatisore, Pintu Angin, km-14 road of

PT. Kaltim Hutama, c. 500 m a.s.l., Feb. 2001, *Heatubun et al.* 330 (holotype K!; isotypes AAU!, MAN!).

HABITAT. This palm grows in limestone hill forest at an altitude *c*. 500 m above sea level.

VERNACULAR NAME. Warita (Jamur dialect); Mojigre (Kwatisore dialect); Nibung (Indonesian dialect in Papua, also used for other tree palms).

USES. Stems and leaves are used as materials to construct traditional houses (flooring and thatch).

CONSERVATION STATUS. Endangered (EN B2a – c). *Cyrtostachys excelsa* meets criteria B2a – c for threat category "Endangered" (IUCN 2001) because its area of occupancy is less than 500 km² occurring only on a limestone hill in Kwatisore, Nabire, Indonesian Province of Papua. Furthermore, forest in that area was heavily disturbed by logging activities.

NOTES. Cyrtostachys excelsa is the only species in the genus with grouped leaflets (irregularly arranged leaflets), concolorous when dried. This species, together with *C. elegans*, has inflorescences branched to 4 orders, the highest number of branching orders in the genus — the other species being branched to 2 and 3 orders. Also *C. excelsa* is the only species from the Papuasian region that has pink to reddish purple inflorescences, like *C. renda* from west Malesia.

The crown of *Cyrtostachys excelsa* is quite distinct, being composed of a small number of leaves (c. 7), forming a shuttle-cock shape and porrect leaflets, with flattened lowest leaf and other leaves slightly recurved near the tips.

The specific epithet for this species came from the Latin word *excelsus* which means lofty or high, reflecting the impression of the palm when first seen by the author.

5. Cyrtostachys glauca *H. E. Moore* (1966: 86). Type: Papua New Guinea, Morobe Province, Morobe district, forested slopes along logging road just beyond bridge over Markham R. on the road to Bulolo, March 1964, *Moore* 9272 (holotype BH!; isotype LAE).

Slender to moderate, clustering tree palm to 5.5-15 (-21.6) m, with up to c. 3 adult stems and up to 4 or more suckers at base, crown spherical in outline. Stem 5-15 cm diam., bright green and becoming grey in age, nodal scars conspicuous; internodes 3.5-7.5 cm long. Leaves 6-8 in crown, leaves spreading, 172-410 cm long (including petiole); sheath tubular, 66-130 cm long, 8-22 cm wide, forming a distinct crownshaft, 70-240 cm long, bright glaucous, sparsely and minutely lepidote with membranous brown scales; petiole green, elongate, 25-88 (-100) cm long, 2-3 cm wide and 1-1.6 cm thick at the base, rounded and rather densely and minutely brown lepidote below, concave and similarly lepidote or puncticulate above; leaflets regularly

arranged, papery, 45 – 67 leaflets on each side, middle leaflets $58 - 99 \times 3 - 5$ cm, apical leaflets 12. $5 - 24 \times$ 0.5 - 2.5 cm, briefly pointed and sometimes notched at apices, green, discolorous when dried, glaucous adaxially, glaucous to whitish abaxially, with thick, brown membranous ramenta, discontinuous along mid-vein on abaxial surface; rachis with similar lepidote indumentum as petiole. Inflorescence infrafoliar, strongly divaricate, 50 -130 cm long, 100 - 200 cm wide, branched 3 - 4 (mostly)3) orders, green to pale yellow in colour and pale brown to whitish-green when dried; peduncle very short to 5 cm; rachillae 25 - 50 cm long; 2 - 4 mm diam., white, calvx persistent when fruits fallen; pits superficial to shallow, 3-5 pits per 1 cm rachilla length, pit 2-3 mm diam. Staminate flowers $2.5 - 3.2 \times 2.5 - 2.8$ mm; sepals $2 - 2.5 \times 2 - 2.3$ mm; petals $2.2 - 2.9 \times 1.8 - 2.1$ mm; stamens 9 - 10; filaments $0.9 - 2 \times 0.1 - 0.3$ mm; anthers $1.3 - 1.5 \times 0.5 - 0.8$ mm; pollen size, long axis 35 -45 μm, short axis 23 – 41 μm, proximal wall thickness $3~\mu m$, distal wall thickness $3~-~4~\mu m$, tectum surface verrucate, trichotomosulcate grains absent; pistillode $1.1 - 1.8 \times 0.4 - 0.5$ (1 - 1.5 at the base) mm. Pistillate flowers $3 - 3.5 \times 2.5 - 3$ mm; sepals $2.8 - 3 \times 2.8$ mm; petals $2.7 - 3.1 \times 2.5 - 3$ mm; gynoecium $1.5 - 2.5 \times$ 0.5 – 1.5 mm (including 3 recurved stigmas); staminodes 3, membranous. Fruits $9 - 12 \times 4 - 6$ mm, ellipsoid to sickle-shaped, green to black; beak 1 – 4 mm long. Seeds $5 - 7 \times 3 - 4 \times 3 - 4$ mm, ellipsoid, rounded apical and flattened basally. (Figs. 3A - C, 7).

DISTRIBUTION. Cyrtostachys glauca is a Papua New Guinean species. This palm is distributed in Morobe, Milne Bay and Central Provinces.

SPECIMENS EXAMINED. PAPUA NEW GUINEA. Central Province; Yamu road, c. 15 km NE of Cape Rodney, 30 m a.s.l., Sept. 1969, Pullen 8212 (L!, LAE); Pullen 8231 (BH!, CANB, L!, LAE); Yamu village near Mori R., Sept. 1969, Pullen 8198 (BH, CANB, L!, LAE,). Milne Bay Province; along Kabawawa highway, 0 m a.s.l., March 2000, Barfod et al. 454 (AAU!, BRI, CANB, K!, LAE); Esa'ala, Ferguson Island, E of Lake Lavu, 100 m a.s.l., Nov. 1976, Croft et al. LAE 68805 (BRI, L!, LAE); Maiyu R., c. 16 km WNW of Biniguni airstrip, c. 280 m a.s.l., June 1972, Pullen 8409 (A, CANB, L!, LAE,). Morobe Province; forested slopes along logging road just beyond bridge over Markham R. on the road from Lae to Bulolo, March 1964, Moore 9272 (holotype BH!); Lae, Garagos logging road, Katik LAE 62219 (BRI, L!, LAE); Bulili Ridge, near Lababia guest house, 50 − 400 m a.s.l., Kjaer & Magun 512 (AAU!, BRI, CANB, K!); just before Gwabadik on the 4WD track, 275 m a.s.l., Feb. 1993, Takeuchi 8770 (A!, L!, LAE); NW of Waria R., Buttress Ridge above Wara Pao, near Yai Village, c. 200 m a.s.l., July 1999, Takeuchi et al. 13217 (A!); Lae, 60 m a.s.l., Sept.1971, Essig & Katik LAE 55009 (CANB, L!, LAE,); LAE 62219 (L!, LAE).

CULTIVATED. Lae Botanic Garden, main palm collection, Nov. 2006, *Baker & Fazang* 1309 (K, LAE).

HABITAT. Growing in primary forest or secondary forest with scattered subsistence gardens in lowlands to sloping terrain or hill forest at an altitude 30 – 400 m above sea level.

VERNACULAR NAME. *Vekintambu* (Lababia dialect; Morobe), *Hek* (Madang dialect).

USES. Stem for building purposes.

CONSERVATION STATUS. Data Deficient (DD). Although this palm has a relatively wide distribution in SE Papua New Guinea, suggesting the category "Least Concern", more accurate data related to distribution of, and the threats to, this species are still needed to assess its conservation status.

NOTES. Cyrtostachys glauca is easily distinguished from all other species by its spherical crown, glaucous leaf sheath and crownshaft, slender and elongate petioles of more than 50 cm long (– 100 cm), papery leaflets, slender inflorescence and rachilla with sparse superficial pits, and by the unique presence of trichotomosulcate pollen grains.

This is a very peculiar species within *Cyrtostachys* because of the nature of the pits along the rachilla. The pits are very shallow or even lacking in a few specimens (*Kjaer & Magun* 512 and *Barfod* 454) and together with the tiny flowers (in bud) the species may be superficially confused with *Heterospathe* or *Rhopaloblaste*. However, the generic characters such as presence of a crownshaft, connate petals and stamens in staminate flowers, and fruit and seed morphology still clearly indicate it as a species of *Cyrtostachys*.

- **6. Cyrtostachys loriae** *Becc.* (1905: 303). Type: Papua New Guinea, Owen Stanley Range Province, 1887, *Hartmann* s.n. (holotype FI!).
- Cyrtostachys kisu Becc. (1914a: 289); synon. nov. Type: The Solomon Islands, Faro island, Guppy 235 (holotype K!).
- Cyrtostachys peekeliana Becc. (1914b: 28); synon. nov. Type: Papua New Guinea, New Ireland, Peekel 106 (holotype B†; isotype FI!).
- Cyrtostachys brassii Burret (1935: 328); synon. nov. Type: Papua New Guinea, Central Province, Kubuna, Nov. 1933, Brass 5600 (holotype B†; isotype A!).
- Cyrtostachys phanerolepis Burret (1936: 324); synon. nov. Type: Papua New Guinea, Morobe, Sattleberg, July 1935, Clemens 1353 (holotype B†; isotype L!, K, photo!).
- Cyrtostachys microcarpa Burret (1939: 203); synon. nov. Type: Papua New Guinea, Western Province, Fly R., Lake Daviumbu, Sept. 1936, Brass 7757 (holotype A; isotype L!).

Robust, solitary tree palm to 10 - 30 m. Stem 11.5 - 30 cm diam., brownish-grey to whitish below and

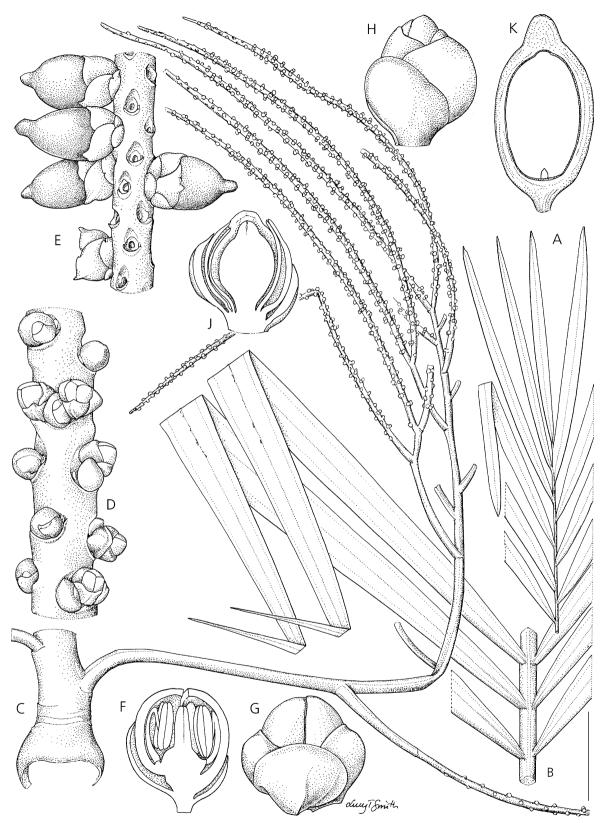


Fig. 7. *Cyrtostachys glauca*. A apical portion of leaf; B middle portion of leaf; C portion of inflorescence; D detail of rachilla with flowers in bud; E portion of rachilla in fruit; F, G staminate flower whole and in section; H, J pistillate flower whole and in section; K fruit in section. Scale bar: A, B = 8 cm; C = 6 cm; D, K = 5 mm; E = 1 cm; F, G = 2 mm; H, J = 2.5 mm. A – B, H – J from *Kjaer* 512, C – D, F – G, K from *Moore* 9272. DRAWN BY LUCY T. SMITH.

green to olive-green above, nodal scars conspicuous, internodes 3 - 30 cm long, crown hemispherical in outline. Leaves 8 – 14 in crown, leaves spreading, 250 – 480 cm long (including petiole); sheath tubular, 112.5 - 180 cm long, 25 - 68 cm wide, forming distinct crownshaft, 125 - 200 cm long, pale yellow to light green; petiole almost missing to short (1 - 10 cm)long), 3 - 5.5 cm wide and 1 - 2.8 cm thick at the base, with thin or thick brown to whitish-purple lepidote indumentum; rachis with similar indumentum as the petiole; leaflets regularly arranged, leathery, 76 – 189 leaflets on each side, middle leaflets $80 - 152 \times 3.4 -$ 6.8 cm, apical leaflets $14 - 50 \times 0.8 - 2$ cm, briefly pointed and sometimes notched at apices, green, discolorous when dried, glaucous adaxially, glaucous to whitish abaxially, fine brown ramenta discontinuous along mid-vein on abaxial surface. Inflorescence infrafoliar, strongly divaricate, 43 - 150 cm long, up to 250 cm wide, branched to 3 orders, green to pale yellow, light brown to black when dried; peduncle very short to 10 cm; rachillae 25 - 88.5 cm long; 6 - 9 mm diam., brown to rusty brown, calvx persistent after fruits fallen; 8 - 16 pits per 1 cm rachilla length (in various stages), pits 2 – 6 mm in diam., deep. Staminate flowers $2.5 - 4 \times 2 - 3$ mm; sepals $1.2 - 2.2 \times 1.5 - 2.9$ mm; petals $2 - 3 \times 1.2 - 2.5$ mm; stamens 9 - 13; filaments $0.7 - 3.5 \times 0.1 - 0.2$ mm; anthers $1 - 1.5 \times 0.5 -$ 0.8 mm; pollen size, long axis 27 - 56 µm, short axis $25 - 48 \mu m$, proximal wall thickness $1.5 - 5 \mu m$, distal wall thickness 1 – 5 μm, tectum surface sparsely verrucate and gemmate, trichotomosulcate grains present; pistillode $0.7 - 1.7 \times 0.2 - 1$ (1 - 1.5 at the base) mm. Pistillate flowers $2-6 \times 2.2-5.5$ mm; sepals $2.5 - 5.2 \times 2.1 - 6.2$ mm; petals $1.5 - 5.2 \times 1 - 5$ mm; gynoecium $1 - 5 \times 0.5 - 3.5$ mm (including 3 recurved stigmas); staminodes triangular (3 – 4) to circular, membranous. Fruits 8 - 16 × 4 - 5 mm, ellipsoid to sickle-shaped, green to black; beak 0 – 2 mm long. Seeds $5 - 8 \times 2 - 5 \times 2 - 5$ mm, ellipsoid to ovoid, rounded apically and flattened basally. (Figs. 3D – H, 8).

DISTRIBUTION. Cyrtostachys loriae is a widespread species in the Papuasian region, distributed from Kepala Burung (Bird Head's Peninsula) in the west to Solomon Islands in the east.

SPECIMENS EXAMINED. INDONESIA. West Papua Province: Manokwari distr.; Ransiki subdistr., Ransiki, *Kostermans* s.n. (BO!). Papua Province: Yapen distr.; Yapen Island, Yapen Tengah Mts. Natural Reserves, near base camp at Mananayang R., c. 500 m a.s.l., Feb. 2005, *Heatubun et al.* 546 (BO!, K!, MAN!); Trans Yapen road, first slope from Mananayang R. to Serui, c. 550 m a.s.l., Feb. 2005, *Heatubun et al.* 547 (BO!, K!, MAN!). Mimika distr., Timika, mile 50 on road to Tembagapura, forest to W of container depot, 545 m a.s.l., Feb. 1998, *Heatubun et al.* 208 (BH!, BO!, K!, L!, MAN!). Sarmi distr., Mamberamo R., Idenburgh R., Bernard

Camp, 55 m a.s.l., April 1939, Brass 13807 (A!, L!); Bernard Bivak (Camp), 50 m a.s.l., Meijer Dress 501 (BO!, L!). Jayapura distr., Cyclops Mts, N Cyclops Mts. Natural Reserves, 50 – 700 m a.s.l., Jan. 2001, Desianto 01 (AAU, K!, MAN!); foot path to Raveni summit, c. 790 m a.s.l., Aug. 1998, Heatubun et al. 279 (BO!, FTG!, K!, L!, MAN!). Keerom distr., Arso, Tami R., Treferer, 100 - 150 m a.s.l., March 2002, Gusbager et al. 23 (K!, LAE!, MAN!); Workwana village, Yumseyus, 50 – 100 m a.s.l., Feb. 2005, *Heatubun et al.* 527 (BO!, K!, MAN!); Heatubun et al. 532 (BO!, K!, MAN!); Heatubun et al. 533 (BO!, K!, MAN!). Merauke distr., Kwell village, 60 m a.s.l., Sept. 2000, Maturbongs 654 (BO!, AAU, K!, MAN!); Bot R., about half-way between Bupul and Lake Wam, 60 m a.s.l., Aug. 1954, van Royen 4734 (A!, BO!, L!). PAPUA NEW GUINEA. Sandaun Province: Miwaute, Nov. 1996, Barfod et al. 395 (AAU!). Western Province: Palmer R., 2 miles below junction Black R., July 1936, Brass 7162 (A!, L!); Middle Fly R., Lake Daviumbu, Sept. 1936, Brass 7757 (A, L!); c. 2 miles N of Kiunga, Upper Fly R., c. 300 m a.s.l., Sept. 1967, Pullen 7305 (BH, CANB, L!, LAE,). East Sepik Province: Sepik distr.; along the Sepik R. between Ambunti and Malu, 50 m a.s.l., May 1966, Hoogland & Craven 10114 (A!, BH, CANB, K!, L!, LAE); Anggoram subdistr.; Wewak - Anggoram area, 4 miles N of Timbunke mission, 30 m a.s.l., Sept. 1959, Pullen 1692 (CANB, K!, L!, LAE). West Sepik Province: Sepik distr., Aitape subdistr.; along Pieni R. near Walwali Village, 30 m a.s.l., June 1961, Derbyshire & Hoogland 8020 (A, K!, L!). Telefomin distr.; Carpentaria Exploration Co. Frieda R. Camp, 60 m a.s.l., April 1978, Essig & Young LAE 74052 (CANB, L!, LAE); Hak Valley, c. 900 m a.s.l., Morren & Frodin 3189 (K!). Southern Highlands Province: Lake Kutubu, near Tage, 90 m a.s.l., Sept. 1961, Schodde 2248 (CANB, K!,). Gulf Province: Kikori distr.; TFI logging concession, near Morare village, 20 km NE of Kikori, 130 m a.s.l., Nov. 2000, Baker et al. 1110 (AAU, BRI, K!, L, LAE, NY); logging camp on Vailala R., 0 m a.s.l., March 2000, Barfod 478 (AAU!, BRI, K!, LAE); Barfod 482 (AAU!, BRI, K!, LAE, CANB). Morobe Province: Sattleberg, 700 m a.s.l., July 1935, Clemens 1353 (K (photo)!, L!). Milne Bay Province: Mullins bay road, 0 m a.s.l., March 2000, Barfod et al. 463 (AAU!, BRI, K!, LAE, CANB). Central Province: Kuriva, 300 m a.s.l., March 2000, Barfod 467 (AAU!, BRI, K!, LAE, CANB); Koitaki, 50 m a.s.l., Carr 12253 (A, BM, L!); Kairuku subdistr.; c. 15 miles W of Maipa Village on Akaifu R., Sept. 1962, Derbyshire 867 (CANB, L!, LAE). New Ireland Province: New Ireland Island, Peekel 444 (FI!, K (photo)!). North Solomon Province: Bougainville Island, Marmarromino, 50 m a.s.l., Oct. 1930, Kajewski 2220 (A!). THE SOLOMON ISLANDS. Fauro island; Guppy 235 (holotype K!); Eastern Peninsula; 200 m a.s.l., April 1964, Whitmore BSIP 3945 (BSIP, K!); New Georgia group; Baga Island, April 1964, Whitmore BSIP 4210 (BSIP, K!).

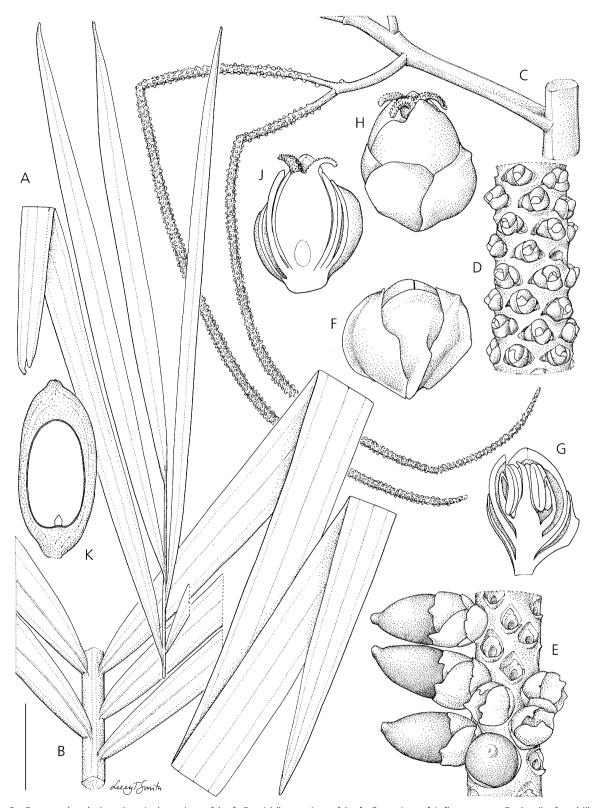


Fig. 8. *Cyrtostachys loriae.* A apical portion of leaf; B middle portion of leaf; C portion of inflorescence; D detail of rachilla; E portion of rachilla in fruit; F, G staminate flower whole and in section. H, J pistillate flower whole and in section; K fruit in section. A – B, from *Baker* 1110, C, D, H, J from *Heatubun* 208, E – G, K from *Hoogland & Craven* 10144. Scale bar: A, B, C = 8 cm; D, E = 1 cm; F, G = 2 mm; H, J = 3 mm; K = 7 mm. DRAWN BY LUCY T. SMITH.

HABITAT. This palm grows in primary or secondary forest in the lowlands or hill forest at an altitude of 30 - 400 m above sea level.

VERNACULAR NAMES. Papua Indonesian: tnang nyi (Sentani, Jayapura); gap (Marap, Tami R.); terep/terrip (Yei/Je, Merauke); Nibung (Indonesian dialect in Papua, also used for other tree palms). Papua New Guinea: yomberi (Timbunke, Sepik); yowoh (Waskuk, Sepik); hek/he-ek (Amele, Madang); terep (Jal, Madang); apaku (Mekeo, Maipa); flim (Mianmin); lobu (Wapi, Marok); mun (Orme, Walwali); wai eba (Kutubu); toono-i (Bougainville Island); a ikul (New Ireland Island). Solomon Islands: kwara'ae (Aatarae).

USES. Cyrtostachys loriae is one of the more useful species in the genus from an ethnobotanical point of view. It has been used traditionally by people native in both New Guinea and the Solomon Islands. The stems and leaves are used as building materials for traditional houses, e.g. piles, flooring, water pipes, thatch and mattresses. The palm heart or "cabbage" is also eaten fresh or cooked.

CONSERVATION STATUS. Least Concern (LC). *Cyrtostachys loriae* is widespread in the Papuasian region, and as yet the conservation status of this species seems not to be a cause for concern. However, land conversion for oil palm plantations or other purposes, including illegal logging activities in West New Guinea (Indonesian Provinces of Irian Jaya Barat and Papua) could have a severe effect on the populations of the palm. Detailed population studies are still needed to assess its conservation status more precisely.

NOTES. Cyrtostachys loriae was the first species of the genus to be published from the Papuasian region (Beccari 1905). This palm is easily distinguished by its solitary and robust habit, spherical crown, pendulous leaflets, very short (– 10 cm long) or missing petiole and an inflorescence more robust than in other species, branched to 3 orders, with robust rachillae bearing large and deep pits.

Re-examination of the type specimens of *Cyrtostachys brassii*, *C. kisu*, *C. loriae*, *C. microcarpa*, *C. peekeliana* and *C. phanerolepis* revealed no significant differences among them except those caused by differences in developmental stages, despite the inadequate nature of the specimens. Morphological variation among them is continuous, especially after comparison with more adequate specimens from recent collections. No disjunctions in variation occur that would allow the consistent separation of six species as recognised by previous authors. The narrow species concept used in the past reflects limited information obtained from single collections.

Moore (1966) pointed out his suspicions that the five taxa above might not be distinct; they all have a solitary habit and 12 stamens except for *Cyrtostachys phanerolepis* — six stamens, pits in 9 series and larger fruits (Burret 1936). Burret did not realise that the specimen *Clemens* 1353 (the type of *C. phanerolepis*) had been mixed with some male flowers of *Licuala*, and he

described *C. phanerolepis* with staminate flowers from *Licuala*.

Cyrtostachys loriae is the most widespread species of the genus in the Papuasian region, and also occupies a wide range of ecological conditions from swampy areas in the lowlands to heath forest in lower montane vegetation, from evergreen rain forest to dry areas in savannah lands and from the main island of New Guinea to small off-shore islands and the Solomons. The adaptation to various habitats is reflected in the very variable appearance, a plasticity that occurs not only in size and shape, but also the number of certain organs, such as number of stamens. In some specimens, different numbers of stamens can be found within one inflorescence or in different collections from the same locality.

There are two collections from savannah areas in Merauke, Indonesian Province of Papua, *Maturbongs* 654 and *van Royen* 4734, which look quite distinct in the appearance of their leaves. The petiole and rachis are covered by scaly indumentum, and the leaflets are slender with discolorous surfaces (glaucous adaxially, purplish-brown abaxially). Other characters such as habit, stem, inflorescence and flowers, fruits and seeds fit with *Cyrtostachys loriae*. The variation in leaf character may reflect different ecological conditions in savannah areas.

7. Cyrtostachys renda Blume (1838: 66, 1843: 101). Bentinckia renda (Blume) Mart. (1853: 316). Type: Indonesia, Sumatra, East Sumatra, around Indrapura, Korthals s.n. (lectotype L!, designated here; isolectotype K!).

Areca erythropoda Miq. (1861a: 6). Type: Indonesia, Sumatra, Bangka Island, Djebus, *Teisjmann* s.n. (holotype BO!).

Cyrtostachys lakka Becc. (1885: 141). Type: Malaysia, Borneo, Sarawak, Kuching, Nov. 1866, *Beccari PB* 2674 (lectotype FI!, **designated here**).

Cyrtostachys lakka var. singaporensis Becc. (1885: 141). Type: Singapore,"cultivato nel giardino del Sig. Wham-poa", Anon. (holotype FI!)

Invalid names:

Pinanga purpura Miq. (1861b: 590), nom. inval., in synon. Ptychosperma coccinea Teijsm. & Binn. (1866: 69); nom. nud.

Areca erythrocarpa H. Wendl. in Kerch. (1878: 231), nom. nud.

Pinanga rubricaulis Linden (1885: 61), nom. nud.

Slender, clustering tree palm with up to c. 3 or more adult stems up to 15 (-20) m high. Stem c. 6-10 cm diam., green with greyish stripes or yellow with somewhat greenish and purplish stripes, internodes 15-24 cm long, crown appearing shuttle-cock

shaped. Leaves 7 - 10 in crown, erect, stiff, to 150 cm long; sheath tubular, c. 100 cm long, forming distinct crownshaft, scarlet to bright red, with scattered black thick scales; petiole elongate, 5 - 50 cm long, 1.5 -2.5 cm wide and 1-2 cm thick at the base, channelled adaxially, rounded abaxially, red, indumentum as sheath; leaflets regularly arranged, leathery, 26 - 40 leaflets on each side, $56 - 107 \times 3 - 6$ cm at middle portion, apical leaflets $10 - 20 \times 1 - 2$ cm, briefly pointed with long tip and sometimes notched at apices, green, discolorous when dried, glaucous adaxially, waxy white abaxially, mid-vein with discontinuous membranous brown scales. Inflorescence strongly divaricate, to 90 cm long, branched to 2 (possibly 3) orders, creamy, green to dark purplish-red; peduncle 5 – 8 cm long; rachilla 27 - 73.5 cm long and 4 - 6 mm diam., calyx persistent on rachillae when fruits fallen off; pits 2-5 mm diam., 5-7 pits per 1 cm rachilla length. Staminate flowers $2 - 2.5 \times 2 - 3$ mm, asymmetrical; sepals $1.8 - 2 \times 2$ mm, imbricate, rounded, strongly keeled; petals $1 - 2 \times 1 - 1.8$ mm, triangular, brown at apex and base; stamens 12 - 15; filaments $0.7 - 1 \times$ 0.2 - 0.3 mm; anthers $1 - 1.5 \times 0.5 - 0.8$ mm; pollen size, long axis 36 – 43 μm, short axis 27 – 33 μm, proximal wall thickness 1.5 - 2 μm, distal wall thickness not observed, tectum surface microfossulate-rugulate, trichotomosulcate grains present; pistillode 0.7 - 1 × 0.2-0.5 mm, trifid. Pistillate flowers $4-5\times3-4$ mm; sepals $3 - 4 \times 2 - 3$ mm, imbricate, strongly keeled, dark brown to black; petals $3 - 3.5 \times 2 - 2.5$ mm; gynoecium 3.5 x 1.5 mm (including three recurved stigma 0.5 - 1 mm); staminodes circular, 0.5 - 1 mm height. Fruits $7 - 10 \times 4 - 7$ mm, ellipsoid to ovoid, light green becoming black when ripe. Seeds $4 - 5 \times 3 - 5 \times$ 3 - 5, ellipsoid to ovoid. (Fig. 3J - M).

DISTRIBUTION. This is the only species found to the west of Wallace's Line, occurring in the southern part of Thailand, Malay Peninsula, Sumatra and Borneo.

SPECIMENS EXAMINED. THAILAND. Narathiwat Province: Tak Ban, Phru Kok Daam, March 1985, Niyondham 852 (BKF, K!); Tho daeng, c. 30 km SE of Narathiwat, 50 – 100 m a.s.l., Nov. 1990, Barfod & Ueachirakan 41772 (AAU, BKF, K!, PSU); to Daeng, 75 m a.s.l., Oct. 1996, Barfod et al. 43888 (AAU!, BKF, PSU). N of Sritamerat, Ta Samet, c. 50 m a.s.l., Jan. 1928, Kerr 14332 (K!). SUMATRA. Aceh, Asdat 171 (BO!); Asahan, Polak s.n. (BO!); Bangka Island, Djebus Teysmann s.n. (BO!); Bengkalis, Selat panjang, 3 m a.s.l., Nov. 1919, Bequin 457 (L!, BO!); near Indrapura, Korthals s.n. (L!, K!; the type); Riau, Widyatmoko 399 (BO!); Widyatmoko 400 (BO!); South Sumatra, Dransfield JD 1252 (BO!); Natuna Island, Mogea 2990 (BO!). MALAY PENINSULA. Selangor: Telok swamp forest, Klang, March 1968, Dransfield 713 (K!). SINGAPORE." cultivato nel giardino del Sig. Whampoa", Anon. (holotype FI!). BORNEO. SABAH: Kudat distr., Pulau Balembangan, NE inner side Telok

Lung, 10 m a.s.l., BCS-EFA-LM et. al. SAN 86702 (K!, KEP, L!, SAR, SING); Sandakan, Jan. 1921, Wood 1111 (A!, PNH, SAN). SARAWAK: Kuching, Nov. 1866, Beccari PB 2674 (FI!); 1865 - 1869, Beccari PB 3438 (K!); Bintulu, Sept. 1867, Beccari PB 4038 (FI!); 1929, Clemens 21377 (A!, BO!, K!); Miri distr., Rian road, 50 m a.s.l., April 1959, Saleh 1214 (K!, L!, S, SAR). BRUNEI DARUSSALAM: Belait, Labi, km 20 Labi road, burnt over white sand forest, level land, 50 m a.s.l., March 1992, Dransfield ID 7279 (K!); Bukit Bakong, Oct. 1992. Bernstein 278 (K!): Maruntungan, May 1932. Keith 2491 (K!). CULTIVATED. Indonesia: North Sumatra, Sibolangit Botanic Garden, 500 m a.s.l., Sept. 1927, Lörzing 12083 (L!); West Java, Bogor Botanic Garden, origin from Banka Island, loc. V. K. 37, April - May 1936, Furtado SFN 3/1/68 (BO!, K!, L!, SING); loc. V. G. no. 4., May 1903, Schoute s.n. (L!); Jan. 1906, n.n. (L!); n.n. (BO!). Malaysia: Penang Botanic Garden, Sept. 1900, Curtis 3527 (K!). UK: Royal Botanic Gardens Kew, Palm House, May 1998, 1982-5882 (K!). Seychelles: Victoria, Mali, Dec. 1971, Elizabeth 111 (K!). Singapore: Singapore Botanic Garden, Lawn K, Sept. 1929, Furtado s.n. (K!, SING). Thailand: Peninsular Botanic Garden Khao Chong, Trang, Barfod s.n. (AAU (photo)!).

HABITAT. Cyrtostachys renda grows in lowland peat swamp forest, especially in coastal areas, but more rarely occurs in peat swamps in uplands from 0-500 m above sea level.

VERNACULAR NAMES. Thailand: kap daeng, mark-dang (Thai). Malay Peninsula: pinang rajah (Malay). Sumatra: pinang renda or rende' (Indrapura); pinang rimbou (Sibolga); pinang lempiauw or pinang lepiaw (Bangka island). Borneo: malawaring, raring (Brunei). Trade names: pinang merah, palem merah, (Malay/Indonesia); sealing wax palm, lipstick palm (English); hsing hsing yeh tzu (Chinese); rode palm (Dutch).

USES. This palm has limited traditional uses; stems are used for flooring and leaves for thatch. It is, however, a highly desirable and widely cultivated ornamental for tropical regions.

CONSERVATION STATUS. Vulnerable (VU). See Dransfield & Johnson (1991), Kiew (1991), and Mogea (1991) for conservation status assessment.

NOTES. Cyrtostachys renda differs from all other species in the bright red crownshaft and leaf sheath, the lowest number of leaflets (26 – 40 on each side), the leaflets being waxy white abaxially, the inflorescence branched mostly to 2 orders (possibly up to 3), the tectum surface of pollen rugulate, and its preferred habitat in lowland peat swamp forest in southern Thailand, Malay Peninsula, Sumatra and Borneo.

In the protologue of *Cyrtostachys renda*, no material is cited although a reference is made to Blume's account in *Rumphia*, published some years later, in which the Korthals specimen is mentioned (Blume 1838, 1843). We formally designate this specimen as

lectotype. In the case of *C. lakka*, Beccari (1885) cited two specimens, *Beccari* PB 2674 and 4038, both of which are extant at FI. Harold E. Moore annotated *Beccari* PB 2674 (FI) as lectotype in 1956, but to our knowledge did not publish this lectotypification. We have formalised this typification here. The transfer of *Cyrtostachys lakka* to a synonym of *C. renda* has already been made by Whitmore (1982).

The bright green stems and brilliant red to orange crownshafts make *Cyrtostachys renda* a highly desirable and widely cultivated ornamental. Infraspecific taxa have been described from cultivation and the number of these could increase in parallel to horticultural demand. Ellison & Ellison (2001) introduced two cultivars, *C. renda* 'Apple' and *C. renda* 'Orange Crownshaft', followed by Waddel (2002) with his *C. renda* 'Theodora Buhler'. Before them, Tucker (1992) reported, that in Singapore Botanic Garden grew *C. renda* 'Ruby' and that it was one of the most treasured specimens of all, and he also discussed a strange brown crownshafted form of *C. renda* in Florida. All the cultivars of *C. renda* were described based on different stem and crownshaft colours.

Specimens of Uncertain Affinity

Heatubun 679 & 680 (Cyrtostachys sp.).

This specimen was collected from a plant cultivated at the Kebun Raya Bogor (Bogor Botanic Garden) in the lawn XIB. XX, close to the nursery and plant conservation building. In its reddish sheaths this palm resembles Cyrtostachys renda somewhat but is nevertheless quite distinct. It is a large, clustering tree palm growing to 20 m high with a stem of more than 10 cm diam. with elongate internodes. The crown is hemispherical in outline and the leaves bear pendulous leaflets, a short petiole and a greenish-red to yellowish-red sheath and petiole with a few green stripes. The inflorescence is large, branched to 3 orders (never 2-branched). Although the clustering habit and red leaf sheath suggest characters of C. renda, it is far too robust to match that species. The taxon could well be a result of hybridisation between two different species (C. elegans and C. renda) that have been planted together in the garden (Dransfield 1999). Further studies are required before a new hybrid species can be formally described.

Excluded and Uncertain Names

Cyrtostachys ceramica (Miq.) H. Wendl. in Kerch. (1878: 242) = **Rhopaloblaste ceramica** (Miq.) Burret (1928: 288).

Heterospathe compsoclada (Burret) Heatubun comb. nov. Cyrtostachys compsoclada Burret, Notizb. Bot. Gart. Berlin-Dahlem 13 (118): 325 (1936). Type: Papua New

Guinea, Central Province, Boridi, Sept. 1935, *Carr* 13136 (holotype B†; isotypes K!, L!).

After re-examination of the type of Cyrtostachys compsoclada Burret, no characters diagnostic of Cyrtostachys were found, while all the characters fit with Heterospathe. There are no pits, and the rachillae are covered in thick brown indumentum. In the staminate flowers, petals and filaments are free (connate or united in Cyrtostachys), and stamens 6 in number (8 – 15 in Cyrtostachys). Leaf and leaflets are very small for an adult palm in Cyrtostachys and the flower colour is said to be purple — colourful inflorescences and flowers are known in *Heterospathe*. Moreover, the cited altitude, 5000 feet (1500 m) a.s.l., is higher than usual for Cyrtostachys. The highest recorded altitude for Cyrtostachys being 900 m a.s.l. for C. barbata, whereas Heterospathe is most frequently found at submontane to montane elevations.

Cyrtostachys ledermanniana Becc. (1923: 450). See notes under Cyrtostachys barbata for the discussion.

Acknowledgements

Many individuals and institutes contributed to the completion of this work. We would like to thank the curators and staff of herbaria A, AAU, BH, BO, BRI, FI, K, KEP, L, LAE, MAN, PNH, SAN and SING for access to their specimens, databases and for providing loans in many cases. Dr Hannah Banks is thanked for assistance with pollen laboratory work and microscopy. Dr Sander van der Kaars provided fossil pollen information. Lucy T. Smith prepared the elegant plates.

This research was conducted while CDH did his Master's degree in Institut Pertanian Bogor. CDH would like to thank the Dransfields, the Bakers and the staff of the Herbarium, Royal Botanic Gardens, Kew for their support and hospitality during his recent visits. Special thanks to Marthinus Iwanggin, Piter Gusbager, Herkilaus Rumakewi, Tobias Paiki, Krisma Lekitoo, Piter Matani, Maikel Simbiak, Hermus Indou for help during fieldtrips to Tanah Papua. Financial support came from BPPS DIKTI Depdiknas, local government of Provinsi Irian Jaya Barat and local government of Kabupaten Manokwari, the BAT Biodiversity Partnership to the PONG project of the Royal Botanic Gardens, Kew, the Pacific Biological Foundation, the Sibbald Trust, and the Ethnobotanical Conservation Organisation for South East Asia (ECO-SEA).

List of Specimens Examined and Identified

Species numbers are given in brackets and in bold after collection numbers.

Key: (1) C. bakeri, (2) C. barbata, (3) C. elegans, (4) C. excelsa, (5) C. glauca, (6) C. loriae, (7) C. renda.

Anon (Cult. Singapore) s.n. (7)

Baker et al. 1110 (6), 1138 (1); Barfod 478 (6), 482 (6); Barfod s.n. (7); Barfod & Uechirakan 41772 (7); Barfod et al. 395 (6), 454 (5), 463 (6), 467 (6), 43888 (7); BCS-EFA-LM et al. SAN 86702 (7); Beccari PB2674 (7), PB3438 (7), PB4038 (7); Bernstein 278 (7); Bequin 457 (7); Brass 7162 (6), 7757 (6), 13707 (2), 13807 (6)

Carr 12253 (6); Clemens 1353 (6), 21377 (7); Croft et al. LAE 68805 (5); Curtis 3527 (7)

Desianto 01 (**6**); Derbyshire 867 (**6**); Derbyshire & Hoogland 8020 (**6**); Dransfield JD713 (**7**), JD1252 (**7**), JD7279 (**7**)

Elizabeth 111 (7); Essig & Katik LAE 55009 (5); Essig & Young LAE 74052 (6)

Furtado SFN 3/1/06 (3), 3/1/28 (3), 3/1/68 (7); Furtado s.n. (7)

Guppy 235 (6); Gusbager 23 (6)

Heatubun et al. 194 (3), 208 (6), 279 (6), 330 (4), 341 (3), 527 (6), 532 (6), 533 (6), 546 (6), 547 (6); Hoogland & Craven 10114 (6)

Kajewski 2220 (6); Kanehira & Hatusima 12747 (3), 12851 (3); Katik LAE 62219 (5); Keith 2491 (7); Kerr 14332 (7); Kjaer & Magun 512 (5); Korthals s.n. (7); Kostermans s.n. (6)

Lörzing 12083 (7)

Maturbongs 654 (6); Meijer Dress 501 (6); Mogea 2990 (7); Moore 9272 (5); Morren & Frodin 3189 (6) Niyondham 852 (7)

Peekel 444 (6); Polak s.n. (7); Pullen 1692 (6), 7305 (6), 8198 (5), 8212 (5), 8231 (5), 8409 (5)

Saleh 1214 (7); Schoode 2248 (6); Schoute s.n. (7)

Takeuchi 8770 (5); Takeuchi et al. 13217 (5); Teysmann s. n. (7)

van Royen 4734 (6)

Whitmore BSIP 3945 (6), 4210 (6); Widyatmoko 399 (7), 400 (7); Wood 1111 (7)

References

- Asmussen, C. B. & Chase, M. W. (2001). Coding and non-coding plastid DNA in palm systematics. *Amer. J. Bot.* 88: 1103 1117.
- Bachman, S., Baker, W. J., Brummitt, N., Dransfield, J.
 & Moat, J. (2004). Elevational gradients, area and tropical island diversity: an example from the palms of New Guinea. *Ecography* 27: 299 310.
- Baker, W. J., Coode, M. J. E., Dransfield, J., Dransfield, S., Harley, M. M., Hoffmann, P. & Johns, R. J. (1998). Patterns of distribution of Malesian vascular plants. In: R. Hall, J. D. Holloway & B. R. Rosen (eds.), Biogeography and Geological Evolution of SE Asia. pp. 243 258, Backhuys, Leiden, Netherlands.
- _____ (2000). The Palms of New Guinea Project. *Palms* 44: 160, 165.
- _____ (2002). The Palms of New Guinea Project. *Fl. Males. Bull.* 13: 35 37.

Banka, R. & Baker, W. J. (2004). A monograph of the genus *Rhopaloblaste* (*Arecaceae*). *Kew Bull.* 59: 47 – 60.

- Barfod, A., Banka, R. & Dowe, J. L. (2001). Field guide to palms in Papua New Guinea. AAU reports 40, Department of Systematic Botany, University of Aarhus, Aarhus University Press.
- Barmawidjaya, B. M., Rohling, E. J., van der Kaars, S., Grazzini, C. V. & Zachariase, W. J. (1993). Glacial conditions in northern Molucca Sea region (Indonesia). Palaeogeograph., Palaeoclimat., Palaeoecol. 101: 147 – 167.
- Barrow, S. C. (1998). A monograph of *Phoenix L.* (*Palmae: Coryphoideae*). Kew Bull. 53: 513 575.
- Beccari, O. (1885). Reliquiae Schefferianae: illustrazione di alcune palme viventi nel giardino botanico di Buitenzorg. *Ann. Jard. Bot. Buitenzorg* 2: 6 165.
- ____ (1905). Palme nuove papuane. *Webbia* 1: 303 304.
- ____ (1914a). Manipolo di palme nuove polinesiane conservate nell' ebario di Kew. *Webbia* 4: 289.
- ____ (1914b). Neue palmen Papuasiens. *Bot. Jahrb. Syst.* 52: 28 29.
- ____ (1923). Neue palmen Papuasiens II. *Bot. Jahrb. Syst.* 58: 450 451.
- Blume, C. L. (1838). *Cyrtostachys* Blume. *Bull. Sci. Phys. Nat. Néerl.* 1: 66.
- _____(1838, 1843). Rumphia, vol. 2. Lugduni, Batavorum. Burret, M. (1928). Beiträge zur Kenntnis der Palmen von Malesia, Papua und der Südsee. *Repert. Spec. Nov. Regni Veg.* 24: 253 296.
- ____ (1935). Neue palmen aus Neuguineae III. *Notizbl. Bot. Gart. Berlin-Dahlem* 12: 328 330.
- ____ (1936). Neue palmen aus Neuguineae IV. *Notizbl. Bot. Gart. Berlin-Dahlem* 13 118: 324 325.
- ____ (1937). Neue palmen aus Neuguineae V. *Notizbl. Bot. Gart. Berlin-Dahlem* 13: 472 473.
- ____ (1939). Palme gesammelt in Neu Guinea von L. J. Brass. *J. Arnold Arbor.* 20: 203 204.
- Chapin, M. H., Essig, F. B. & Pintaud, J. C. (2001). The morphological and histology fruits of *Pelagodoxa* (Arecaceae): taxonomic and biogeographical implications. *Syst. Bot.* 26: 779 785.
- Dam, R. A. C., Fluin, J., Suparan, P. & van der Kaars, S. (2001). Palaeoenvironmental developments in the Lake Tondano area. *Palaeogeograph.*, *Palaeoclimat.*, *Palaeoecol.* 171: 147 183.
- Davies, P. H. & Heywood, V. H. (1963). *Principles of angiosperm taxonomy*. Oliver & Boyd, Edinburgh.
- Dransfield, J. (1978). Growth forms of rain forest palms. In: P. B. Tomlinson & M. H. Zimmermann (eds.), *Tropical trees as living systems.* pp. 247 268, Cambridge University Press, Cambridge.
- (1981). Palms and Wallace's Line. In: T. C. Whitmore (ed.), *Wallace's Line and Plate Tectonics*, pp. 43 56, Clarendon, Oxford.
- ____ (1986). A guide to collecting palms. *Ann. Missouri Bot. Gard.* 73: 166 176.

- (1987). Bicentric distribution in Malesia as exemplified by palms. In: T. C. Whitmore (ed.), *Biogeographical Evolution of the Malay Archipelago*, pp. 60 72, Clarendon, Oxford.
- ____ (1999). Species and species concepts in old world palms. *Mem. N.Y. Bot. Gard.* 83: 5 20.
- ____ & Uhl, N. W. (1986). An outline of classification of palms. *Principes* 30: 3 11.
- & Johnson, D. (1991). The conservation status of palms in Sabah (Malaysia). In: D. Johnson (ed.), *Palms for human needs in Asia: Palm utilization and conservation in India, Indonesia, Malaysia and Philippines.* pp. 175 179, WWF Project 3325, Balkema, Rotterdam.
- —, Uhl, N. W., Asmussen, C. B., Baker, W. J., Harley, M. M. & Lewis, C. E. (2005). A new phylogenetic classification of the palm family, *Arecaceae. Kew Bull.* 60: 559 569.
- —, Uhl, N. W., Asmussen-Lange, C. B., Baker, W. J., Harley, M. M. & Lewis, C. E. (2008). *Genera Palmarum*: The evolution and classification of palms. Royal Botanic Gardens, Kew.
- Ellison, D. & Ellison, A. (2001). Cultivated palms of the world. UNSW, Sydney.
- Essig, F. B. (1977). A systematic histological study of palm fruits. I. The *Ptychosperma* alliance. *Syst. Bot.* 2: 151 168.
- ____ (1982). A synopsis of genus *Gulubia. Principes* 26: 159 173.
- ____ (1999). Trends of specialization in the palm pericarp. *Mem. N.Y. Bot. Gard.* 83: 73 77.
- & Young, B. (1979). A systematic histological study of palm fruits II. The *Areca* alliance. *Syst. Bot.* 4: 16 28.
- & Young, B. (1985). A consideration of *Gronophyllum* and *Nengella* (Arecoideae). *Principes* 29: 129 137.
- ______, Manka, T. & Bussard, L. (1999). A systematic histological study of palm fruits III. The Subtribe Iguanurinae (Arecaceae). *Brittonia* 51: 307 325.
- ______, Bussard, L. & Hernandes, N. (2001). A systematic histological study of palm fruits IV. The Subtribe Oncospermatinae (Arecaceae). *Brittonia* 53: 466 471.
- & Hernandes, N. (2002). A systematic histological study of palm fruits V. The Subtribe Archontophoenicinae (Arecaceae). *Brittonia* 54: 65 – 71.
- ____ & Litten, L. (2004). A systematic histological analysis of palm fruits VII. The Cyrtostachydinae (Arecaceae). *Brittonia* 56: 375 379.
- Fisher, J. B. & Maidman, K. J. (1999). Branching and architecture in palms: value for systematics. *Mem. N.Y. Bot. Gard.* 83: 35 46.
- Govaerts, R. & Dransfield, J. (2005). World checklist of palms. Royal Botanic Gardens, Kew.
- Hahn, W. J. (2002). A molecular phylogenetic study of the *Palmae* (*Arecaceae*) based on *atp*B, *rbc*L, and 18S nr-DNA sequences. *Syst. Biol.* 51: 92 – 112.
- Hallé, F. R., Oldeman, A. A. & Tomlinson, P. B. (1976).Tropical trees and forest: an architectural analysis.Springer, Berlin.

- Harley, M. M. (1990). Occurrence of simple, tectate, monosulcate or trichotomosulcate pollen grains within the Palmae. *Rev. Palaeobot. Palynol.* 64: 137 147.
- ____ (1996). Palm pollen and the fossil record. Ph.D. thesis, University of East London.
- ____ (1999). Palm pollen: overview and examples of taxonomic value at species level. *Mem. N.Y. Bot. Gard.* 83: 95 120.
- & Baker, W. J. (2001). Pollen aperture morphology in Arecaceae: application within phylogenetic analyses, and a summary of the fossil record of palm-like pollen. *Grana* 40: 45 77.
- Heatubun, C. D., Walujo, E. B., Mogea, J. P., Purwanto, Y. & Baker, W. J. (In prep.). Ethnobotany of palms in Tanah Papua (Western New Guinea). *J. Trop. Ethnobot.*
- Holmgren, P. K., Holmgren, N. H. & Barnett, L. C. (1990). *Index herbariorum*, eighth ed. New York Botanical Garden, New York.
- Holttum, R. E. (1955). Growth-habits of monocotyledons variations on a theme. *Phytomorphology* 5: 399 413.
- IUCN (2001). *IUCN red list categories and criteria. Version* 3.1. IUCN, Gland, Switzerland.
- Jones, D. L. (1995). Palms throughout the world. Reed Books, Sydney.
- Kerchove, O. (1878). Les Palmiers. Rothschild, Paris.
- Kiew, R. (1991). Palm utilization and conservation in Peninsular Malaysia. In: D. Johnson (ed.), Palms for human needs in Asia: Palm utilization and conservation in India, Indonesia, Malaysia and Philippines. pp. 75 130, WWF Project 3325, Balkema, Rotterdam.
- Lewis, C. E. & Doyle, J. J. (2002). A phylogenetic study of tribe Areceae (Arecaceae) using two low-copy nuclear genes. *Pl. Syst. Evol.* 236: 1 17.
- Linden, J. (1885). Catalogue des Plantes de la Compagnie Continentale d'Horticulture, No 117. Gand, Belgium.
- Maddison, W. P. & Maddison, D. R. (2000). *MacClade version 4.0b10*. Sinauer Associates, Sunderland, Massachusetts.
- Martius, C. F. P. (1853). *Historia naturalis palmarum*. Vol. 3. Weigel, Leipzig.
- McDade, L. A. (1995). Species concepts and problems in practice: insight from botanical monographs. *Syst. Bot.* 20: 606 622.
- Miquel, F. A. W. (1861a). Revue des palmiers de l'île de Sumatra. *J. Bot. Néerl.* 1: 1 29.
- ____ (1861b). Prodromus Florae Sumatranae. Flora van Nederlandsch Indië, suppl 1. van der Post, Amsterdam.
- Mogea, J. P. (1991). Indonesia: palm utilization and conservation. In: D. Johnson (ed.), *Palms for human needs in Asia: Palm utilization and conservation in India, Indonesia, Malaysia and Philippines.* pp. 37 73, WWF Project 3325, Balkema, Rotterdam.
- Moore, H. E. (1966). New palms from the Pacific. *Principes* 10:85-99.
- ____ (1973). The major groups of palms and their distribution. *Gentes Herb*. 11: 27 141.

- Norup, M. V., Dransfield, J., Chase, M. W., Barfod, A. S., Fernando, E. S. & W. J. Baker (2006). Homoplasious character combinations and generic delimitation: a case study from the Indo-Pacific arecoid palms (Arecaceae). *Amer. J. Bot.* 93: 1065 – 1080.
- Pigram, C. J. & Davies, P. J. (1987). Terranes and the accretion history of the New Guinea orogen. BMR *J. Austral. Geol. Geophys.* 10: 193 212.
- Punt, W., Blackmore, S., Nilsson, S. & Le Thomas, A. (1994). *Glossary of pollen and spore terminology*. LPP Contribution Series 1. LPP Foundation, Utrecht.
- Sarkar, S. K. (1970). Palmales. Res. Bull. Cytogen. Lab. Dept. Bot. Univ. Calcutta 2: 22 23.
- Stafleu, F. A. & Cowan, R. S. (1976). *Taxonomic literature*. Vol. I: A G. Bohn, Scheltema & Holkema, Utrecht.
- Swofford, D. L. (1998). PAUP*: Phylogenetic analysis using parsimony (and other methods). Sinauer Associates, Inc., Sunderland, MA.
- Teisjmann, J. E. & Binnendijk, S. (1866). *Catalogus Plantarum quae in Horto Botanico Bogoriensi Coluntur.* Ter Lands-Drukkerij, Batavia (Jakarta).
- Tomlinson, P. B. (1961). *Anatomy of the Monocotyledons*. p. 425, Oxford University Press, London.
- (1990). The structural biology of palms. pp. 99 103, Oxford University Press, London.

- Tucker, R. (1992). Experiences with *Cyrtostachys renda*. *Mooreana* 2: 11 16.
- Uhl, N. W. & Dransfield, J. (1987). Genera Palmarum: A classification of palms based on the work of H. E. Moore Jr. L. H. Bailey Hortorium and International Palm Society, Allen, Lawrence, Kansas.
- Van der Kaars, S., Wang, X., Kershaw, P., Guichard, F. & Setiabudi, D. A. (2000). A late Quaternary palaeoecological record from the Banda Sea, Indonesia: patterns of vegetation, climate and biomass burning in Indonesia and northern Australia. *Palaeogeograph.*, *Palaeoclimat.*, *Palaeoecol.* 155: 135 153.
- Van Welzen, P. C. (1997). Increased speciation in New Guinea: tectonic causes? In: J. Dransfield, M. J. E. Coode & D. A. Simpson (eds.), *Plant Diversity in Malesia III: Proceedings of the 3rd International Flora Malesiana Symposium 1995*. pp. 363 387, Royal Botanic Gardens, Kew.
- Waddel, H. (2002). A new cultivar: *Cyrtostachys renda* 'Theodora Buhler'. *Palms* 46: 70 72.
- Whitmore, T. C. (1973). *Palms of Malaya*. p. 53, Oxford University Press, London.
- ____ (1982). The sealing wax palm. *The Garden* 107: 457.