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A TAXONOMIC REVISION OF THE GENERA *CYCAS* AND *EPICYCAS* GEN. NOV. (CYCADACEAE)

D.J. DE LAUBENFELS¹ & F. ADEMA²

SUMMARY

The genus *Cycas* L is divided into four subgenera, all new, and thirty species are described, of which two are new. A new Asian genus, *Epicycas* de Laub., is recognized for several *Cycas* species and one undescribed species with a subterranean bulbous stem base. Keys to the subgenera of *Cycas* and their species, and to the genus *Epicycas* are given.

Key words: *Cycas*, *Epicycas*, morphology, taxonomy.

INTRODUCTION

The most recent revision of the genus *Cycas* was more than sixty years ago by Schuster (1932) who listed eight species with numerous subspecies and varieties in an almost incomprehensible confusion of categories. Six years earlier Pilger (1924) reported 'approximately 15' species but named only 13. As a matter of fact, over forty species had already been described, at least half of which were perfectly valid. Subsequently more than two dozen more species have been offered, few of which are really new. Several regional monographs [Thailand, Smitinand (1971, 1972); China, Fu et al. (1978); the Philippines, Amoroso (1986); and Queensland, Hill (1992)] have lately added to our knowledge of the genus, but these have not been coordinated with areas outside each treatment. Jones (1993) undertook to describe every possible species of cycad from a horticultural point of view and achieved 44 species in the genus *Cycas*. He did not attempt any analysis and more than one third of his species are duplicates and he missed a few. The genus therefore remains very much in need of revision.

Cycas was originally described by Linnaeus (1737, 1753, 1754) based on a variety of material, much of it cultivated but including references to India, Amboina, and Japan. Later, species were distinguished for Japan (Thunberg, 1784), Cochin China (De Loureiro, 1790), Queensland (Brown, 1810), Bengal (Hamilton, 1825), and Madagascar [Desfontaines (ex Gaudichaud, 1826)]. Confusion began with Roxburgh (1832) who described two species based on material cultivated in Calcutta, said to be from the East Indies. The female specimen attributed to Ambon (specimen in BM) does not correspond to known cycads from there; instead it appears to be *C. silvestris* common further west. The associated male specimens which he described correspond best to *C. javana*, also from further west. He actually described 'two out of three' male specimens but did not describe the third. Clearly, these 'Ambon' cultivars

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represent a mixture. At any rate, Roxburgh identified this material with *C. circinalis*. The material attributed to the Moluccas (also in BM) appears to derive from Orissa Province (India, close to Calcutta) and Roxburgh erected the species *C. sphaerica* for it. It does not help that he thought it would better fit the *Toddapana* of Rheede, upon which *C. circinalis* is based, than does the Ambon material, which he had identified as *C. circinalis*. The result of all this is that it established the erroneous idea that *C. circinalis* is represented from India throughout the East Indies.

In a series of papers, Miquel (1839, 1840, 1842, 1843, 1851, 1868) tried to characterize the genus *Cycas*. First in 1839, among other things, he erected *C. rumphii* and *C. celebica* for the cycads described from Ambon and Celebes by Rumphius (1741), adding in 1840 *C. circinalis* var. *angustifolia* (India), *C. rumphii* var. *timorensis* (Timor), *C. madagascarensis* (Madagascar), and *C. glauca* (cult.). Later, in 1842, he described *C. circinalis* var. *javana* on female material from Java and in 1843 equated Roxburgh's *C. circinalis* with his *C. rumphii*. In 1851 he assigned *C. sphaerica* to *C. circinalis*. Finally, in 1868, he put *C. celebica* and *C. circinalis* var. *javana* into *C. rumphii*, whose description he now altered to correspond to the Java material, a regrettable move because more than one species is clearly involved. However, he again allowed *C. sphaerica* as a distinct species and he asserted that the identification of many cultivars as *C. circinalis* was inappropriate. Miquel's work suggested that *C. rumphii* is quite widespread, more so than is true.

The revision of the genus by Schuster (1932) further confounded the understanding of the genus. By use of subspecies, varieties, and forms, he assembled a large part of the genus *Cycas* into *C. circinalis*. Several other species were put into *C. rumphii*. This has further promoted a broad species concept in the genus so that all kinds of taxa have been treated as *C. circinalis*, various others as *C. rumphii*. However, the subunits of these species are seldom if ever used. No wonder that recent authors express reservations about the identity of many cultivars when provenance is not definitely known.

DIVISION OF CYCAS INTO TWO GENERA

Only recently a group of strikingly different species of *Cycas* in southeastern Asia has become known in detail. Unlike other species put in the genus *Cycas*, these plants arise from a bulbous underground base. Such bases occur in other cycad genera in other families along with emergent trunks but in those genera the emergent trunks are an unmodified continuation of the underground part, or the bulbous bases are not underground at all. In the species of *Cycas* in question the underground bases often eventually do produce an aerial stem of a kind which is slender and not at all a continuation of the underground part.

Schuster (1932) was the first to put the species of *Cycas* with bulbous trunks into a separate section which he named *Indosinensis*, including the two species then known to have this character. Smitinand (1971) distinguished a section *Stangerioides*, based on the presence of a subterranean trunk, to accommodate *C. micholitzii*, leaving out *C. siamensis* because of its well developed aerial trunk. However, the latter has a gigantic, mostly or entirely subterranean bulbous base and just like the former only eventually produces a slender aerial trunk. Two other species of the new genus had

been described before Schuster (1932) described his section, but their underground base was not reported. Unlike for *Cycas* sens. str. our knowledge of the species of the here newly described genus *Epicycas* is quite incomplete, much of what we know has only recently been uncovered and several specialists, particularly from China, are actively studying this material. Therefore the treatment of *Epicycas* will have to be necessarily less complete than that of *Cycas*.

Besides the bulbous base, some other comments can be made concerning the distinctions of *Epicycas*. The pinnules, for example, are characteristically flat, rarely with even the slightest bend to the, often undulate margins, while those of *Cycas* mostly have bent or even revolute margins. In some species of *Epicycas* the pinnules (and comb-teeth) are dichotomized (= with divided apices), a character unknown in *Cycas*. Where known, the pollen cones in *Epicycas* are tapering cylindrical, while those of *Cycas* are mostly ovoid. Otherwise, the two genera are not different.

CYCADACEAE

Palm-like plants with or without underground bulbs, aerial trunks (rarely absent) with a large pith, generally armored with the bases of older leaves. *Leaves* large, pinnately divided, petiole usually with thorns corresponding to the pinnules above. *Pinnules* numerous, \pm linear, base particularly in the lower part of the leaf more or less narrowed, after drying more or less placed in a groove on the rachis, usually somewhat above the center on either side so that the lower side of the rachis is more prominent, apex, when pinnules are at least 15 mm wide, acuminate, apiculate, margin entire, midvein single, prominent. *Cataphylls* in clusters alternating with clusters of leaves or fertile structures, lanceolate, c. 5 cm long, at the base c. 1 cm wide, like the emerging leaves and the fertile structures densely orange-brown tomentose. *Pollen cones* terminal, ovoid or cylindrical, usually tapering, at first compact, elongating to shed pollen, growing point continuing by a lateral bud at the base of the pollen cone; peduncle scaly, c. 2 cm diam. *Microsporophylls* numerous, spirally placed, wedge-shaped, c. 3 cm long, length variable depending on the place within the cone, longer towards the center, with numerous clusters (sori) of pollensacs on the abapical side in a weak left/right division, sori extending from about the base to nearly the widest part, microsporophylls ending in a sterile apical part gradually to abruptly narrowing to an acute to obtuse apex whose margin is turned upwards to the apex of the cone, usually with an acumen or spine at the apical margin, size of the sterile apex and the amount of turning depending on the placement in the cone. *Megasporophylls* clustered like the leaves, rather loosely to somewhat compact, eventually replaced by the continued growth of the apex; each sporophyll with a stalk c. 1 cm wide and variable in length, the lower ones longer, with towards the apex two lateral rows of more or less opposite ovules, megasporophylls ending in a sterile part, this gradually to abruptly expanded, triangular to long-lanceolate, usually with lateral teeth, these sometimes comb-like, resembling pinnules, sterile part ending in a small to large acumen or spike, sometimes with a few reduced teeth at the base. *Ovules* one to several, flattened ovoid (longer than wide, wider than thick), usually glabrous, with a fleshy outer layer and a stony inner layer. *Cotyledons* 2, hypogeal.

KEY TO THE GENERA

- 1a. Subterranean bulbous base absent. Trunks cylindrical, sometimes branched, sometimes slightly enlarged at the base. Margins of pinnules flat or, more often, bent to revolute. Pollen cones usually ovoid **Cycas**
- b. Subterranean bulbous base present. Aerial trunks, if present, slender. Margins of pinnules flat. Pollen cones usually tapering cylindrical. — Pinnules and comb-teeth dichotomously divided into some species **Epicycas**

CYCAS

Cycas L., [Hort. Cliff. (1737) 482] Sp. Pl. (1753) 1188; Gen. Pl. ed. 5 (1754) 495. — Type species: *Cycas circinalis* L.

Short to tall trees with cylindrical, sometimes branched trunks, base sometimes somewhat enlarged, not subterranean. *Leaves* flat or both rows of pinnules raised to form a trough (secund). *Pinnules* undivided, more or less lanceolate, straight or curved, either basally in most species or apically in others, sessile, decurrent, margin flat to revolute; neighboring pinnules usually 2–4 mm apart in the broadest part of the leaf, but more dispersed basally and more crowded apically (when the pinnules are angled apically they can touch one another). *Megasporophylls* without or with teeth in the apical part, teeth up to 3 cm long, often only 1–2 mm long, usually increasing in length towards the acumen or all of the same size; ovules 1–12, often at least 4.

Distribution — Thirty species, from eastern Africa and Madagascar across India to southern China and Japan, throughout the tropical Asian Islands to the Marshall Islands and Tonga, and along the northern and eastern coasts of Australia.

Habitat — In moist to humid environments at low to moderate elevation, from the equatorial rain forest a short distance into the subtropics. Found in the understory of forests, particularly along streams or in open disturbed areas, often where the conditions are seasonal. Probably establishing most commonly in open conditions, but, because of their slow growth and long life, overtaken by larger faster growing trees.

Notes — Several problems complicate the identification of *Cycas* species and need to be considered. The complications are partly due to the slow growth of these plants which may not produce reproductive structures for many years. As a result, many collections are sterile and the pollen structures of several species are not yet properly described. Other problems arise from a natural variability, and the large size of the leaves.

Cycas leaves vary a great deal with age and vigor of a plant. Because of their size or accessibility the largest leaves are rarely collected. Thus, whole leaves, when available in the herbarium, are frequently smaller than reported typical sizes. The number and length of the pinnules also vary with age and vigor, and furthermore pinnules are somewhat shorter towards the upper and lower parts of the leaf. Also the spacing of the pinnules varies from one end of the leaf to the other; loosely spaced basally and more crowded apically. Collectors usually save only a portion of the leaf and different parts of the same leaf may appear in different herbaria. In spite of published reports on spacing of pinnules in various species, a careful study of specimens and all available published data on leaf size and number of pinnules, representing

nearly all species, a remarkable degree of consistency was found in average spacing within a leaf. Published data conflicting with this observation seem to indicate a crowding or even overlap of pinnules, which is not confirmed in this study; overlapping pinnules do not occur. For example, Hill (1992) for *C. media* gives up to 150 pinnules on each side of a leaf, but, a maximum length of 140 cm for the leaf minus the petiole, that is less than 1 cm for each pinnule, yet the pinnules are up to 10 mm wide at the widest part, the median pinnules are 13 mm apart plus 4 mm width at the base. His *C. ophiolitica* is 'more crowded' than *C. media*, and is illustrated so, yet the numbers provided indicate distinctly more space for the pinnules of the former than of the latter. The spacing of the pinnules is hardly ever a distinct character for *Cycas* species. Fortunately, within a species the pinnule width is not particularly variable.

Pinnule apices are often battered or missing in herbaria, however; in only a few species the shape of the apex is significant. Probably all pinnules of *Cycas* plants are originally apiculate. These apiculate tips are often called acuminate which contrasts with the broad acuminate tips with an acumen over 1 cm long that are normal for pinnules more than 15 mm wide. Narrower pinnules are less acuminate, and the narrowest ones have a more or less rounded apex.

The midrib of the pinnules of immature leaves is usually weak, later becoming more prominent, particularly on the underside of the pinnule. In some species the midrib becomes equally or more prominent above than below, while in a few species the midrib never becomes prominent. The upper surface of the midrib may be more or less yellow but this trait is quite variable and appears to result from growing conditions.

The apex of the leaf often has a wedge-shaped or V-shaped gap between the last spreading pinnules while the rachis is terminated by no more than a thin spur or a very reduced pinnule. Equally often there is one pinnule bent into a terminal position. Sometimes there may even be 2 or 3 or more progressively strongly reduced pinnules spreading laterally and a smaller one terminal. Considerable variation is seen in adjacent leaves and although a progressive strong reduction of apical pinnules may be more common in species as *C. revoluta* and *C. taitungensis*, it is by no means always present, not even in these species.

The amount of narrowing of the base of a pinnule varies along a rachis. It is largest at the base of the leaf and may sometimes almost form a petiolule, further apically the base is broader and more strongly decurrent. Specimens representing portions of a leaf will obviously vary in this character depending on the part of the leaf they derive.

Much emphasis has been put by some authors on thorns on the leaf petiole being present or not. Probably no species has always thornless petioles and leaves with petioles with some thorns can be found on the same plant with thornless ones. The tendency to have few or no thorns, however, is a significant trait. When the leaf base is cut off by a collector, as it usually is, this trait cannot be seen. Or worse, the small part remaining may have thorns but the missing part may or may not, and the impression may be misleading.

Cycas ovules mature into a fruit containing a stony seed covered by a fleshy coat some 4–5 mm thick. Immature, undersized fruits with a much thinner coat are often collected. Also, all dried specimens have the coats reduced to a thin wrinkled covering. The whole structure (seed + coat) is commonly seen as a seed. However, confusion is often caused because collectors rarely specify what they mean: fresh or dried, with or without the coat, 'seed' size reported or not.

Pollen cones of cycads are often difficult to obtain and tend to disintegrate after shedding pollen. Before shedding they are compact but in shedding they elongate and the diameter shrinks (see Krempin, 1990: 226, a photo of *C. pruinosa* with both stages). When shedding the microsporophylls often are reflexed basally. Immature cones will shed pollen when dried, and immature specimens are often collected and described. The result is that the dimensions given for pollen cones are quite unreliable.

Other variable traits can be noted. Pinnule margins are usually revolute; however, the amount of bending varies from specimen to specimen and also with age. Clearly, narrower pinnules are more markedly revolute. The two rows of pinnules may be widely spread out to form a flat leaf or they may approach each other to form a trough; pressing leaves in drying, however, may well obscure this character. Leaf glaucousness is not readily evident in dried specimens and is often very inconstant. The number of ovules of a megasporophyll varies a great deal within a species and even within one cluster. Normally, only one or two megasporophylls are included in a herbarium specimen. The length of apical spines on fertile scales can vary quite a bit from base to apex of a pollen cone.

SUBDIVISION OF THE GENUS

Only limited attempts have been made so far to subdivide the genus *Cycas*, mostly by separating one or two species from the rest. Miquel (1843) split off *C. revoluta* (adding in 1849 *C. inermis*) on the basis of linear, revolute pinnules. In 1868 he made this division more formal but without any group name, distinguishing *C. revoluta* by tomentose ovules. Pilger (1926), also without any group names, separated the species with more than two ovules per megasporophyll from those with only two. Unfortunately his information was incorrect. He further subdivided the first group into groups with pectinate or not pectinate megasporophylls. Schuster (1932) described three sections, giving them regional names. His section *Asiorientales* characterized by, amongst others, linear pinnules and cuneate microsporophylls included only *C. revoluta*. His section *Indosinensis* with bulbous trunk bases, linear-lanceolate leaves, and sphenoid microsporophylls included two species: *C. siamensis* and *C. nicholitzii*. All other *Cycas* species were included into section *Lemuricae* with subacuminate pinnulae and acuminate microsporophylls. The section *Indosinensis* will be included in the new genus *Epicycas*.

Recently suggested generic subdivisions continue to be less than satisfactory. Dehgan & Yuen (1983), working with cultivated material, suggested a division of the genus into two groups based on the buoyancy of the seeds. According to them three widespread species have buoyant seeds. One of these is *C. circinalis* which most certainly does not have buoyant seeds. Probably the material they studied was misidentified. Although several species of *Cycas* do have buoyant seeds, closely related ones do not. Dehgan (1987) proposed, but did not describe, groupings identified only by their type species. All his subgenera and sections have names inadmissible according to taxonomic rules. The use of subsections by Schuster (1932) and others will not be discussed here because they add little to our understanding of the genus.

However, several characters used in these suggestions for the subdivision of *Cycas* seem to be useful and will be used, along with certain other characters, for a formal division of the genus *Cycas* into four subgenera.

KEY TO THE SUBGENERA

- 1a. Apex of megasporophylls entire, dentate or serrate; longest lateral teeth up to 6 mm long (rarely a little longer) 2
- b. Apex of megasporophylls pectinate; longest lateral teeth 6–45 mm long 3
- 2a. Sterile apex of microsporophylls triangular, gradually or abruptly curving towards the apex of the pollen cone **Subg. Cycas** (p. 357)
- b. Sterile apex of microsporophylls truncate, abruptly bent towards the apex of the pollen cone **Subg. Truncata** (p. 367)
- 3a. Midveins of pinnules prominent on the upper side. Petioles 25–70 cm long (mostly well over 40 cm long) **Subg. Pectinata** (p. 375)
- b. Midveins of pinnules flat or only slightly prominent at the upper side. Petioles up to 40 cm long (mostly less than 30 cm long) **Subg. Revoluta** (p. 382)

Subgenus Cycas

Cycas L. sect. *Lemuricae* J. Schust. in Engl., Pflanzent. 99 (1932) 65. — Type species: *Cycas circinalis* L.

Trunks slightly enlarged at the base above the ground. *Petioles* with or without thorns. *Pinnules* straight or curving towards the base of the leaf or some curving towards the apex, at least 4 mm wide, margins flat or slightly revolute. Sterile apex of *microsporophylls* acuminate, gradually or abruptly curved upwards. Sterile apex of the *megasporophylls* dentate or serrate, teeth progressively more prominent towards the apex, up to 6 mm long (usually much less, rarely slightly longer), short- to long-acuminate.

Distribution — Nine species from Madagascar and the east coast of Africa to Australia and S New Guinea.

Habitat — Mostly in open places in tropical forests and savannahs, usually under distinctly seasonal conditions.

Notes — The species of this subgenus from India and Australia have much in common.

In this subgenus only *C. thouarsii* from Madagascar and nearby areas and apparently also from Sri Lanka has buoyant seeds.

KEY TO THE SPECIES

- 1a. Seeds without a spongy layer, usually not more than 46 × 39 mm 2
- b. Seeds with a thick spongy layer, at least 54 × 42 mm **3. C. thouarsii**
- 2a. Sterile apex of microsporophylls gradually curving towards the apex of the cone 3
- b. Sterile apex of microsporophylls abruptly bent at the tip 4
- 3a. Sterile apex of microsporophylls lanceolate to slightly acuminate. Longest lateral teeth of the apex of megasporophylls 2–4 mm long **1. C. circinalis**
- b. Sterile apex of microsporophylls strongly acuminate. Longest lateral teeth of the apex of megasporophylls 4–6 mm long **2. C. sphaerica**
- 4a. Pinnules glabrous below 5
- b. Pinnules rusty tomentose below **9. C. furfuracea**

- 5a. Apical part of the megasporophyll mostly over 2 cm wide, when as much as 5 cm long about 3 cm wide, marginal teeth pointing towards the apex, especially near the apex, there at least 4 mm long 6
 b. Apical part of the megasporophylls less than 2 cm wide, marginal teeth spreading, even at the apex, there about 2 mm long **8. *C. normanbyana***
- 6a. Pinnules straight or bent towards the base of the leaf 7
 b. Pinnules bent towards the apex of the leaf, particularly near the apex 8
- 7a. Pinnules 11–28 cm long, 6–9 mm wide **4. *C. media***
 b. Pinnules 6–15 cm long, 5–7 mm wide **5. *C. armstrongii***
- 8a. Trunk base distinctly enlarged. Leaves V-shaped; pinnules 4–7 mm wide, bent upwards on both sides of the rachis to form a trough, midrib stronger below, margin bent **6. *C. angulata***
 b. Trunk base not enlarged. Leaves flat; pinnules (5–)6–8(–11) mm wide, midrib equal above and below, margin flat **7. *C. lanepoolei***

1. *Cycas circinalis* L. — Map 1

Cycas circinalis L., Sp. Pl. (1753) 1188; Lam., Ill. Gen. 5 (1799) t. 891; Rich., Comment. Bot. de Conif. & Cycad. (1826) 187, p.p., t. 24; Hook., Bot. Mag. 55 (1828) t. 2826, 2827; Blume, Rumphia 4 (1849) 13, t. 176; Parl. in DC., Prodr. 16, 2 (1868) 526; Dyer in Hook. f., Fl. Brit. India 5 (1888) 656; J. Schust. in Engl., Pflanzenr. 99 (1932) 66, t. 10 A, F–G; D.D. Pant, Cycas and the Cycads, ed. 2 (1973) 34, t. 8–12; Wijnands, Acta Hort. 182 (1986) 70; K.D. Hill, Taxon 44 (1995) 25. — Lectotype (Stevenson in Jarvis et al., 1993: 40): *Toddapana s. Monta-panna*, Rheede, Hort. Malab. 3 (1682) t. 19.

Cycas undulata Desf. ex Gaudich. in Freyc., Voy. Autour du Monde 1817–1820, Bot. 19 (1826) 433, cult.

Cycas squarrosa Lodd. ex Loudon, Hort. Brit. (1830) 403, cult.

Cycas circinalis L. var. *angustifolia* Miq., Comm. Phytogr. (1840) 119. — *Cycas wallichii* Miq., Monogr. Cycad. (1842) 32. — Lectotype (here designated): *Gaudichaud s.n.* (P; 'given to Wallich'), cult. Calcutta.

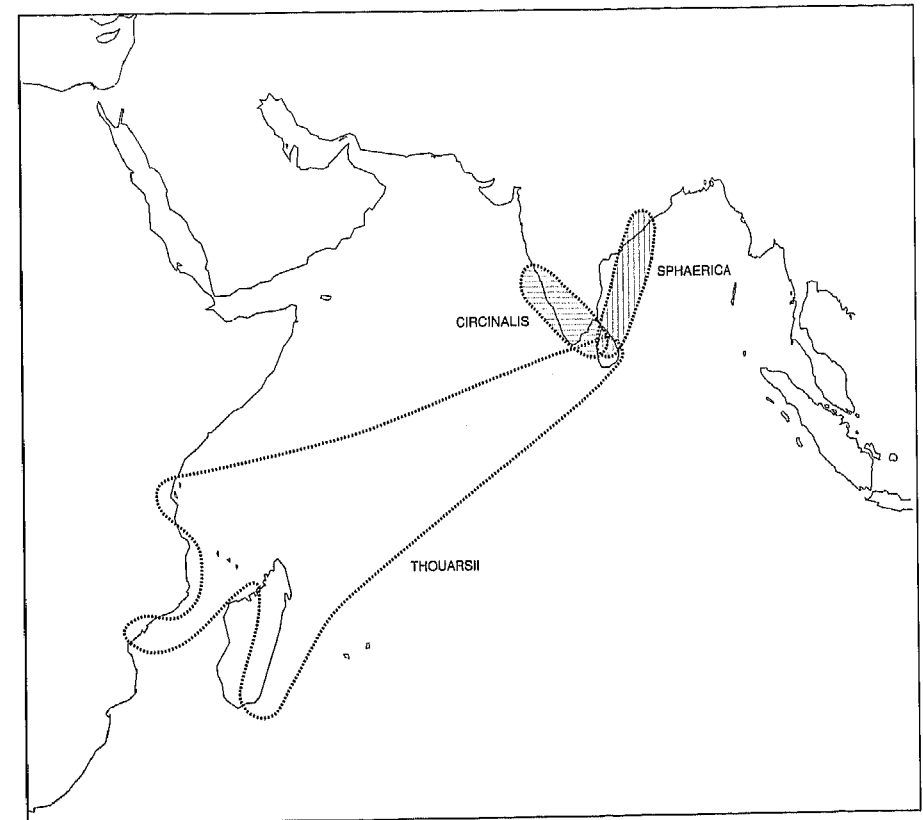
Cycas squamosa Lodd. ex Dyer, Gard. Chron. 16 (1881) 270, cult.

Trunks up to 8 m high, 27–43 cm diam., tapering, often branched. *Leaves* 150–270 cm long, pinnules 80–180 per side; petiole 40–60 cm long, thorns present for most of the length. *Pinnules* lanceolate, 14–27 × 0.7–1 cm, margin distinctly but not strongly bent, midrib more prominent below, green above, lighter below. *Pollen cone* cylindric, slightly tapering, 30–45 × 8–11 cm; peduncle c. 5 cm long. *Microsporophylls* c. 12 mm wide, sterile apex lanceolate or slightly acuminate, 20–45 mm long, gradually curving towards the apex of the cone. *Megasporophylls* with 3–10 ovules; sterile part triangular, 40–60 × 20–25 mm, strongly acuminate, marginal teeth 12–19 per side, 1–2 (lower) to 2–4 (upper) mm long, acumen 10–30 mm long, usually with a few reduced, rather widely spread teeth at the base. *Seeds* ovoid, dull orange or reddish yellow, c. 38 × 31 mm.

Distribution — India (Kerala), Sri Lanka.

Habitat — In dry deciduous forests, sometimes in wet hill forest. Altitude up to 1070 m.

Notes — Although Linnaeus (1753) referred to several places, he indicated India as the habitat for this species; for plants from the other places mentioned by him new species have been described, leaving '*Toda pana*' as the lectotype for *C. circinalis*.



Map 1. Distribution of *Cycas circinalis* L., *C. sphaerica* Roxb., *C. thoursii* Desf. ex Gaudich.

According to Desfontaine (ex Gaudichaud, 1826) *C. undulata* was of unknown origin but very much like *C. circinalis*. As far as we can tell no cultivar with undulate leaves has ever produced reproductive material, furthermore it appears that undulate-leaved horticultural forms have sprung from a variety of species. It remains uncertain which one of these was the plant that Desfontaine had in mind. However, specimens collected by Gaudichaud are in the Paris herbarium and the only one without a specific wild origin is the type of *C. wallichii*, a synonym of *C. circinalis*. Miquel (1840) influenced by the description of Indonesian material by Roxburgh as *C. circinalis*, and by his own var. *javana*, understood *C. circinalis* to have wider pinnules, so, when he saw a true example in Paris, he named it var. *angustifolia* which he later raised to species rank as *C. wallichii*. Subsequently, he became uncertain about the relationship of this species placing it first with *C. rumphii* (Miquel, 1849), and later with *C. pectinata* (Miquel, 1868). The Gaudichaud specimen 'given to Wallich' in the Paris herbarium is evidently the specimen he had in mind and is chosen as the lectotype. Obviously, *C. squarrosa* of Loddiges became mutated to *C. squamosa*. When Dyer (1881) mentioned the latter he gave no reference or description, but cited Wendland who said that it was introduced from Travancore in 1824.

As was mentioned above, the name *C. circinalis* has been applied to so many different things that most citations of it without provenance have to be disregarded.

2. *Cycas sphaerica* Roxb. — Map 1

Cycas sphaerica Roxb., Fl. Ind. 3 (1832) 147; Miq., Linnaea 17 (1843) 693; Tijdschr. Wisk. Natuurk. Wet. 2 (1849) 287; Arch. Néerl. Sci. Exact. & Nat. 3 (1868) 230. — Lectotype (Hill, 1995): *Roxburgh s.n.* (BM), cult. Calcutta.

Cycas circinalis L. var. *orixensis* Haines, Bot. Bihar & Orissa 6 (1924) 1228; K.D. Hill, Taxon 44 (1995) 25. — Lectotype (here designated): *Haines 5876* (K), India, Mals of Puri.

Cycas nathorstii J. Schust. in Engl., Pflanzenz. 99 (1932) 76, t. 10E; K.D. Hill, Taxon 44 (1995) 27. — Type: *Thwaites 3689* (holo G; iso A, K, P).

Trunks up to 4.5 m high, 25–40 cm diam. *Leaves* 150–270 cm long, pinnules 90–180 per side; petiole 27–60 cm long, thorns present for most of the length. *Pinnules* lanceolate, 19–32 × 0.9–1.2 cm, margin more or less flat, midrib more prominent below, green above, lighter below. *Pollen cone* cylindrical, slightly tapering, up to 45 × 10 cm; peduncle not known. *Microsporophylls* 15–22 mm wide, sterile apex acuminate with a narrow spine, 20–45 mm long, bent at the base, then curving sharply upwards. *Megasporophylls* with 3–12 ovules; sterile part triangular, 25–45 × 20–30 mm, acuminate, marginal teeth 16–18 per side, rather widely spreading, 2–4 (lower) to 4–6 or more (upper) mm long, acumen 10–25 mm long, usually with several reduced teeth at the base. *Seeds* ovoid, orange, c. 38 × 30 mm.

Distribution — India (Orissa Prov.), Sri Lanka.

Habitat — Disturbed areas and open forests with substantial rainfall. Altitude low to moderate.

Note — Generally similar to *C. circinalis* differing in the shape of the microsporophylls, the larger teeth on the megasporophyll and the somewhat larger pinnules. Roxburgh's specimen originated without doubt from Orissa; however, he was under the impression that it derived from the Moluccas. Haines (1924) claimed for the var. *orixensis* that the apical spine of the microsporophylls towards the apex of the pollen cone is bifid or trifid, but no specimens are available to confirm this.

3. *Cycas thouarsii* Desf. ex Gaudich. — Map 1

Cycas thouarsii Desf. ex Gaudich. in Freyc., Voy. Autour du Monde 1817–1820, Bot. 19 (1826) 434; R. Br., Prodr. (1810) 347, nomen; Eichler, Nat. Pflanzenfam. 2, 1 (1889) 21; Stapf, Kew Bull. Misc. Inf. 2 (1915) 1; Melville, Fl. Trop. East Afr. (1958) 1, t. 1; de Laub., Flore de Madagascar et des Comores: Gymnosperms (1972) 4, t. 1; photo 2; D.L. Jones, Cycads of the World (1993) 159. — *Cycas circinalis* L. subsp. *thouarsii* (Desf. ex Gaudich.) Engl., Pflanzenw. Afrikas 2 (1908) 82. — Type: *Du Petit-Thouars s.n.* (holo P), Madagascar.

Cycas circinalis auct. non L.: Thouars, Hist. Veg. (1804) 2, t. 1–11; Rich., Comment. Bot. de Conif. & Cycad. (1826) 187, p.p., t. 25, 26; Engl., Pflanzenw. Ost-Afrikas (1895) 422.

Cycas madagascariensis Miq., Comm. Phytogr. (1840) 127. — *Cycas circinalis* L. subsp. *madagascariensis* (Miq.) J. Schust. in Engl., Pflanzenz. 99 (1932) 73. — Lectotype (here designated): Thouars, Hist. Veg. (1804) t. 1.

Cycas comorensis Bruant, Bull. Soc. Bot. France 35 (1888) 246. — Type: *Boivin 2891* (P), Comores.

Cycas rumphii Miq. subsp. *zeylanica* J. Schust. in Engl., Pflanzenz. 99 (1932) 75, t. 10C, D, 11K–M. — Type: *Thwaites 3862* (holo G; iso BM, GH, K).

Trunks up to 10 m high, up to 45 cm diam., tapering, often branched. *Leaves* 150–300 cm long, pinnules 60–120 per side; petiole 30–50 cm long, thorns present for most of the length. *Pinnules* lanceolate, 17–31(–35) × 0.8–1.3(–1.5) cm, margin slightly bent, midrib more prominent below, green above, lighter below. *Pollen cone* cylindrical, slightly tapering, 30–60 × 10–15 cm; peduncle up to 5 cm long. *Microsporophylls* 15–17 mm wide, sterile apex slightly acuminate, 12–15 mm long, tip 5–8 mm long, sharply hooked. *Megasporophylls* with 4–10 ovules; sterile part lanceolate, 60–80 × 20–25 mm, strongly acuminate, marginal teeth 5–13 per side, weakly developed (lower) to 2–3 mm long (upper), acumen 10–30 mm, with reduced teeth at the base. *Seeds* red, 54–60 × 42–50 mm, buoyant.

Distribution — East coast of Madagascar, Comores, East coast of Africa (Zambesi delta), Sri Lanka.

Habitat — Strand vegetation in rain forest environments and lowland rain forest. Altitude at least up to 500 m.

Note — Generally similar to *C. circinalis*, differing in the fertile structures, the somewhat wider pinnules, and especially the large, buoyant seed. Sri Lankan material appears to be similar to that of Madagascar, the localities on the latter island are far distant from all others for the genus, leading to the suspicion of a Sri Lankan origin. The strand habitat and the buoyancy of the seeds have not been confirmed in Sri Lanka. There are two possible mechanisms for transport across the Indian Ocean; 1) Seeds could have crossed by floating. However, many suitable islands and coasts between Madagascar and Sri Lanka lack this species. Using these areas as stepping stones seems not to have occurred. 2) The other possibility is human transport as an edible crop. Even now *C. thouarsii* is in Madagascar locally used as a cultivated edible plant.

4. *Cycas media* R. Br. — Map 2

Cycas media R. Br., Prodr. Fl. Nov. Holl. (1810) 348; Miq., Linnaea 17 (1843) 687; Arch. Néerl. Sci. Exact. & Nat. 3 (1868) 233; Parl. in DC., Prodr. 16, 2 (1868) 527; K.D. Hill, Telopea 5 (1992) 184, t. 3; D.L. Jones, Cycads of the World (1993) 145, photos on p.145, 146. — Type: *R. Brown 3106*, p.p. (holo BM), Australia, Calder Isl.

Cycas gracilis Miq., Versl. en Meded. Akad. Wetensch. Amsterdam 15 (1863) 366. — Type: *F. Mueller s.n.* (holo U), Australia, Cape Upstart.

Cycas kennedyana F. Muell. ex Warb., Monsunia 1 (1900) 181, t. 7, f. a [Warb., Melbourne Chemist and Druggist 4 (1885) 41, nomen]. — Type: *Fitzalan s.n.* (holo MEL, n.v.), Australia, Normanby Ranges.

Cycas megacarpa K.D. Hill, Telopea 5 (1992) 188, t. 5, f. 5a–c; D.L. Jones, Cycads of the World (1993) 147, photos. — Type: *Hill & Stanberg 4142* (holo NSW, n.v.), Australia, Port Curtis Distr.

Trunks up to 5 m high, 10–20 cm diam., sometimes branched. *Leaves* 90–180 cm long, pinnules 80–150 per side, the two rows sometimes forming a trough; petiole 30–60 cm long, thorns absent or present up to halfway. *Pinnules* lanceolate, 11–28 × 0.6–1 cm, margin flat to distinctly bent, midrib more prominent below, mid green, sometimes glaucous. *Pollen cone* ovoid, 15–25 × 10–13 cm; peduncle c. 5 cm long. *Microsporophylls* 14–18 mm wide, sterile apex narrowed, 8–18 mm long, spine 6–10 mm long, sharply upturned. *Megasporophylls* with 2–10 ovules; sterile part triangular,

40–70 × 20–30 mm, distinctly acuminate, marginal teeth 12–20 per side, 2–3 (lower) or up to 6 (upper) mm long, acumen 10–30 mm long, with a few reduced teeth at the base. *Seeds* ovoid, orange-yellow to orange-red, 30–40 × 25–36 mm.

Distribution — Australia, along the coasts of Queensland, rarely more than 100 km inland.

Habitat — Open seasonal forest, sometimes in rain forest.

Note — *Cycas circinalis* and *C. media* are quite similar. However, the latter is less robust, has a hooked, not gradually bent apex of the microsporophyll, fewer thorns on the petiole, and a shorter pollen cone. Typical *C. media* may have glabrous, flat pinnules and flat leaves, but these characters show variation throughout its range. By contrast, glaucous pinnules, bent pinnule margins, and pinnule rows forming a trough are commonly seen. For example, the type specimen of *C. gracilis* has distinctly bent pinnule margins. Hill (1992) reports these characters for 'intermediate' populations with respect to *C. platyphylla* (*C. angulata*) near Atherton and the common occurrence of a trough in plants from the northern part of Cape York Peninsula. But these traits could as well represent genetic drift from *C. cairnsiana* or other species. Hill (l.c.) further reports that the southernmost populations of *C. media* have larger seeds (40–60 × 35–45 mm, as *C. megacarpa*); this might merit treatment as a variety if it is consistent.

5. *Cycas armstrongii* Miq. — Map 2

Cycas armstrongii Miq., Archiv. Néerl. Sci. Exact et Natur. 3 (1868) 235; D.L. Jones, *Cycads of the World* (1993) 130, photos p. 130, 131. — Type: *Armstrong 380* (holo U; iso K, P), Australia, Northern Territory, Port Essington.

Cycas papuana F. Muell., *Papuana Pl.* 4 (1876) 71; Warb., *Monsunia* 1 (1900) 180, t. 7, f. e; D.L. Jones, *Cycads of the World* (1993) 151; K.D. Hill, *Austral. Syst. Bot.* 7 (1994) 532, f. 3A, 5. — *Cycas circinalis* L. subsp. *papuana* (F. Muell.) J. Schust. in Engl., *Pflanzenr.* 99 (1932) 70. — Lectotype (Hill, 1994): *D'Albertis s. n.* (holo MEL; iso K), Papua New Guinea, Fly River.

Trunks up to 4 m high, 10–20 cm diam. *Leaves* 90–130 cm long, pinnules 90–125 per side; petiole 15–58 cm long, thorns present up to halfway or absent. *Pinnules* lanceolate, 6–15 × 0.5–0.7 cm, margin flat, midrib equally prominent on both sides, mid to dark green above, lighter below. *Pollen cone* ovoid, 12–21 × 8–12 cm; peduncle c. 5 cm long. *Microsporophylls* 13–20(–23) mm wide, sterile apex 12–18 mm long, narrowed, spine sharply upturned, 5–7 mm long. *Megasporophylls* with 2–6 ovules; sterile part triangular, 35–55 × 20–30 mm, distinctly acuminate, marginal teeth 7–10 per side, 2 (lower) to 4 (upper) mm long, acumen 10–20 mm long, with few reduced teeth at the base. *Seeds* ovoid, yellow or orange, 30–40 × 25–30 mm.

Distribution — Australia, northern part of Northern Territory, southwestern part of Papua New Guinea.

Habitat — Open savannah forest at low elevation.

Note — Very similar to *C. media*, differing in the smaller pinnules with the midrib not prominent below. These characters are not clearly separating the two species and *C. armstrongii* could easily be treated as a variety of *C. media*.

6. *Cycas angulata* R. Br. — Map 2

Cycas angulata R. Br., Prodr. Fl. Nov. Holland (1810) 348; Miq., *Linnaea* 17 (1843) 686; Arch. Néerl. Sci. Exact. & Nat. 3 (1868) 233; K.D. Hill, *Teloepa* 5 (1992) 202, t. 17; D.L. Jones, *Cycads of the World* (1993) 128, photos p. 128, 129. — Type: *R. Brown 3106*, p.p. (holo BM; iso K), Australia, prob. Gulf of Carpentaria, Bountiful Island.

Cycas ophiolitica K.D. Hill, *Teloepa* 5 (1992) 190, t. 7; D.L. Jones, *Cycads of the World* (1993) 150, photos p. 149. — Type: *Hill & Sternberg 4140* (holo NSW, n.v.), Australia, New South Wales, Port Curtis district.

Cycas platyphylla K.D. Hill, *Teloepa* 5 (1992) 193, t. 9, f. 9e (taken from the type); D.L. Jones, *Cycads of the World* (1993) 152, photos. — Type: *Hill & Sternberg 3764* (holo NSW, n.v.), Australia, Queensland, Cook distr., near Petford.

Cycas couttsiana K.D. Hill, *Teloepa* 5 (1992) 197, t. 13; D.L. Jones, *Cycads of the World* (1993) 140, photo. — Type: *Hill & Sternberg 3738* (holo NSW; iso K), Australia, Queensland, Burke distr., Upper Stawell River.

Cycas brunnea K.D. Hill, *Teloepa* 5 (1992) 200, t. 15; D.L. Jones, *Cycads of the World* (1993) 133, photos on p. 134. — Type: *Maconochie 1661* (holo DNA; iso K), Australia, Queensland, Burke distr., Lawn Hill Creek.

Cycas arnhemica K.D. Hill, *Teloepa* 5 (1994) 693, t. 1. — Type: *Maconochie 1477* (holo NSW; iso K), Australia, Northern Territory, Goyder River Crossing.

Cycas orientis K.D. Hill, *Teloepa* 5 (1994) 696, t. 3. — Type: *Hill & Sternberg 3936* (holo NSW, n.v.), Australia, Northern Territory, east of Badalngarrmirri Creek.

Cycas canalis K.D. Hill subsp. *carinata* K.D. Hill, *Teloepa* 5 (1994) 700, t. 4e–g (figures taken from the type). — Type: *Hill & Sternberg 4063* (holo NSW, n.v.), Australia, Northern Territory, 90 km from Stuart Highway on Dorisville Road.

Cycas desolata P.I. Forst., *Austrobaileya* 4 (1995) 345, f. 1–5. — Type: *Forster 14671B* (holo BRI, n.v.), Australia, Queensland, NW of Charters Towers.

Cycas badensis K.D. Hill, *Teloepa* 7 (1996) 20, f. 9 (f. 9b, d, g taken from the type). — Type: *Clarkson 4007* (holo BRI, n.v.), Australia, Queensland, Badre Island.

Cycas maconochie K.D. Hill, *Teloepa* 7 (1996) 48, f. 22. — Type: *Hill & Anderson 4461* (holo NSW, n.v.), Australia, Northern Territory, Mandorah Rd. at Bynoe Harbour Turnoff.

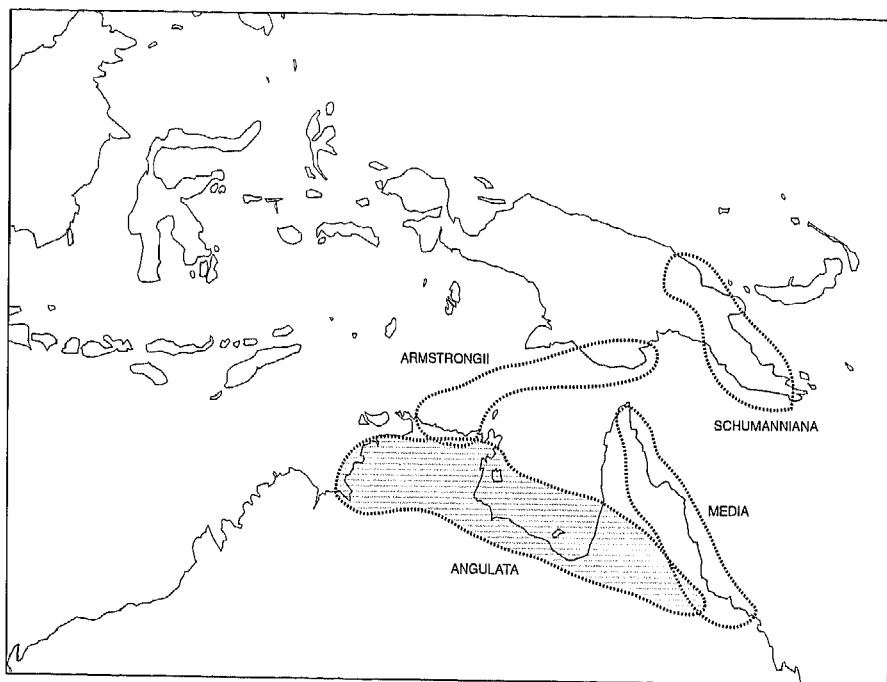
Cycas semota K.D. Hill, *Teloepa* 7 (1996) 23, f. 11 (f. 23 taken from the type). — Type: *Hill & Stanberg 4708* (holo NSW, n.v.), Australia, Queensland, Banaga district.

Cycas tuckeri K.D. Hill, *Teloepa* 7 (1996) 20, f. 10 (f. 10b taken from the type). — Type: *Hill & Stanberg 4683* (holo NSW, n.v.), Australia, Queensland, Coen district.

Cycas yorkiana K.D. Hill, *Teloepa* 7 (1996) 18, f. 8 (f. 8a, b, d–f taken from the type). — Type: *Hill & Stanberg 4711* (holo NSW, n.v.), Australia, Queensland, 20.5 km N of Wenloch R. crossing, Bamaga Rd.

Cycas pruinosa auct. non Maconochie: D.L. Jones, *Cycads of the World* (1993) photographs on p. 102, 103.

Trunks up to 12 m high, often much shorter, base of trunk 25–40 cm diam., occasionally branched. *Leaves* 90–200 cm long, pinnules 80–160 per side, often forming a distinct trough; petiole 15–60 cm long, thorns present up to halfway. *Pinnules* 6–19(–23) × 0.4–0.6(–0.7) cm, apex often bent towards the apex of the leaf at an angle of less than 60°, margin occasionally flat to mostly bent downwards, midrib more prominent below, green above, lighter below, usually glaucous. *Pollen cone* ovoid, up to 45 × 12 cm; peduncle c. 5 cm long. *Microsporophylls* 10–15(–20) mm wide, sterile apex acuminate, 10–17 mm long, with a sharply bent subulate tip mostly c. 8(–20) mm long. *Megasporophylls* with 4–12 ovules; sterile part triangular, 30–55 × 15–27 mm, acuminate, marginal teeth 5–13 per side, 2–3 (lower) to c. 4 (upper) mm long, acumen 10–30 mm long, spike-shaped. *Seeds* yellow to orange, 30–46 × 25–39 mm.



Map 2. Distribution of *Cycas media* R. Br., *C. armstrongii* Miq., *C. angulata* R. Br., *C. schumanniana* Lauterb.

Distribution — Australia, from southern Queensland all the way across Northern Territory, generally within 100 km of the coast.

Habitat — Sparse grassy woodland, often in sandy soil.

Notes — The usually glaucous pinnules often curving apically and mostly forming a trough contrast with *C. armstrongii*. However, more reliable is the midrib of the pinnule that is more prominent below, with the pinnules placed at an angle in the horizontal plane and not perpendicular to the rachis, as well as the enlargement of the trunk base. These characters are entirely intermediate between *C. armstrongii* (and *C. media*) and *C. cairnsiana* suggesting some sort of hybrid origin; this is strengthened by the lack of consistency in these characters. It would appear that *C. angulata* is more widespread than has been realized. In this connection Hill (1992, 1994, 1996) has recently proposed about a dozen new species and several subspecies for populations within the range of *C. armstrongii* and *C. media* that correspond closely to *C. angulata*. He relies on distinctions that tend to be unreliable, but are often selected for horticultural purposes, such as color or density variations in the indumentum of emerging leaves, degree of glaucousness, sharpness of the trough formed by opposite rows of pinnules, amount of revoluteness, and color of leaves. Characteristically, *C. angulata* has white and orange-brown hairs (trichomes) in the tomentum of new leaves; this is, however, variable (the tomentum on cataphylls and megasporophylls is much less variable). In some populations ('*C. brunnea*') white hairs are scarcely evident, while in others ('*C. couttsiana*, *C. orientis*, *C. arnhemica*') it is predominant. The cataphylls are dense-

ly woolly in *C. badensis*, *C. maconochie*, *C. ophiolitica*, *C. platyphylla*, and *C. yorkiana*. Glaucousness is a notoriously variable trait and tends to correlate with habitat. The same can be true of leaf color. After reviewing a large number of specimens, we find the amount of revoluteness, if any, and the sharpness of the trough, if any, variable everywhere. Hill reports that for most of his species the cataphylls are soft and blunt (as in *C. cairnsiana*) rather than pungent (as in *C. angulata*, *C. armstrongii*, and *C. media*). For the time being we must place these species in synonymy pending further testing of their validity. Hill (1992) reports a larger seed for *C. angulata* sens. strict., but all of the seeds we have seen are of similar size and not that large.

7. *Cycas lanepoolei* C.A. Gardner — Map 3

Cycas lanepoolei C.A. Gardner, For. Dept. Bull. Perth 32 (1923) 30, t. E; D.L. Jones, *Cycads of the World* (1993) 143, photos on p. 144. — *Cycas media* R. Br. var. *lanepoolei* (C.A. Gardner) J. Schust. in Engl., *Pflanzenr.* 99 (1932) 78. — Type: *Gardner 1444* (holo W Aust. Forest Dept. Herb., photo seen), Australia, Western Australia, Kimberley Distr., NE of Mt Hann, near source of Moran River.

Cycas spec. 'Pine Creek' Krempin, *Palms and Cycads around the World* (1990) photo p. 226; D.L. Jones, *Cycads of the World* (1993) 162.

Cycas conferta Chirgwin & Wigston, *J. Adelaide Bot. Gard.* 15 (1993) 147; D.L. Jones, *Cycads of the World* (1993) photo on p. 125. — Type: *G. Brown s.n.* (holo DNA, n.v.), Australia, Northern Territory (1981).

Cycas canalis K.D. Hill, *Teloepa* 5 (1994) 698, t. 4a–d (f. 4c taken from the type). — Type: *Hill & Stanberg 4034* (holo NSW, n.v.), Australia, Northern Territory, 31.4 km from Labelle Downs homestead on track to Channel Point.

Cycas xipholepis K.D. Hill, *Teloepa* 7 (1996) 32, f. 15 a–d, f, g taken from the type). — Type: *Hill & Stanberg 4712* (holo NSW, n.v.), Australia, Queensland, Cook Distr., 10.5 km W of Telegraph Line Rd on Batavia Downs to Indley Rd.

Trunks up to 6 m high, 7–23 cm diam. *Leaves* 60–120 cm long, pinnules 80–180 per side; petiole 14–30 cm long, mostly entirely covered with thorns. *Pinnules* 10–20 × (0.5–)0.6–0.8(–1.1) cm, straight or apex bent towards the apex of the leaf, margin flat, midrib weak and equal above and below, mid to deep green and glaucous. *Pollen cone* ovoid, 22–33 × 12–15 cm; peduncle c. 3.5 cm long. *Microsporophylls* 20–23 mm wide, sterile apex acuminate, 8–14 mm long, with a sharply bent subulate tip, 11–18 mm long. *Megasporophylls* with 2–4 ovules; sterile part triangular, 40–65 × 22–32 mm, acuminate, marginal teeth 6–10 per side, 2–3 (lower) to 4 (upper) mm long, acumen up to 30 mm long. *Seeds* yellowish, glaucous when young, 32–42 × 30–36 mm.

Distribution — Australia, northeastern corner of Western Australia and northern parts of Northern Territory.

Habitat — Dry stunted woodland on gravelly or sandy soil.

Note — The short relatively broad and flat apically bent pinnules of *C. lanepoolei* are unusual among the species with apically bent pinnules. In some ways this species resembles *C. media* and *C. calcicola*, being some kind of close relative to them and possibly of hybrid origin. The seed in *C. conferta* is reported to be large and pear-shaped. Overall the original description of *C. conferta*, involving unusual variation in pinnule width and number of thorns on the petiole, suggests that more than one taxon may be involved. Without more material it will be difficult to say whether the rather

wide and crowded pinnules illustrated in Krempin (1990) and Jones (1993) represent a distinct taxon or just an extreme form. Teeth on the megasporophyll are sometimes reported to be absent (see discussion under *C. normanbyana*).

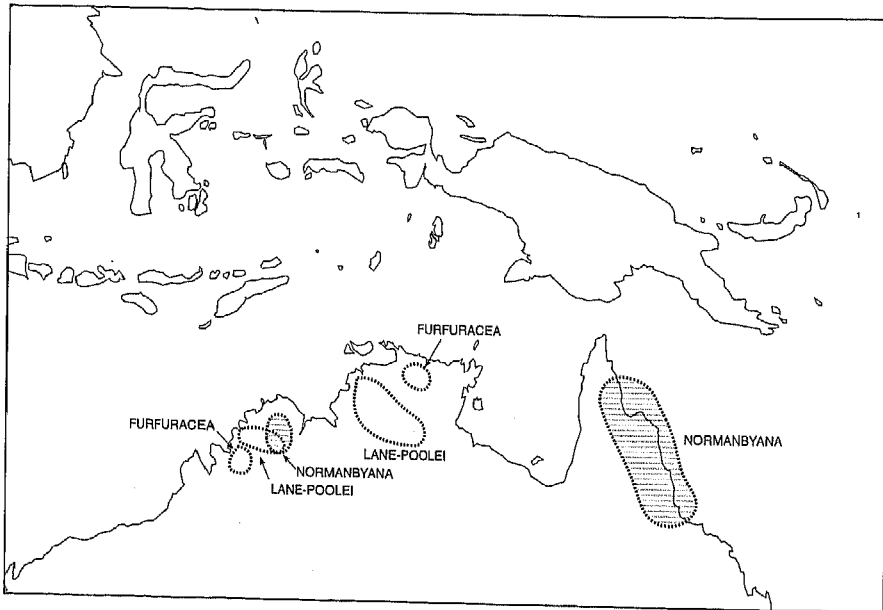
8. *Cycas normanbyana* F. Muell. — Map 3

Cycas normanbyana F. Muell., Fragm. Phytogr. Austr. 8 (1874) 169; Wieland, Amer. Fossil. Cycads 1 (1906) f. 1260 (after Mueller). — *Cycas rumphii* Miq. subsp. *normanbyana* (F. Muell.) J. Schust. in Engl., Pflanzenr. 99 (1932) 75. — Type: *Fitzalan s.n.* (holo MEL 68048; iso K), Australia, Burdekin River.

Cycas basaltica C.A. Gardner, For. Dept. Bull. W Austr. 32 (1923) 31; D.L. Jones, Cycads of the World (1993) photo on p. 131, 132. — *Cycas media* R. Br. var. *basaltica* (C.A. Gardner) J. Schust. in Engl., Pflanzenr. 99 (1932) 78. — Type: *Gardner 1490* (holo W Austr. Forests Dept. Herb., photo seen), Australia, Western Australia, Kimberley Distr.

Trunks up to 6 m high, base conspicuously enlarged, 25–40 cm diam. (in W Australia up to 110 cm). *Leaves* 65–129 cm long, pinnules 70–120 per side; petiole (9–)21–28 cm long, without or with few thorns. *Pinnules* 10–20 × 0.6–0.8 cm, straight or very slightly bent towards the apex of the leaf, margin flat or slightly bent, midrib weak, light to mid green. *Pollen cone* conical ellipsoid, 20–30 × 9–13 cm; peduncle c. 5 mm long. *Microsporophylls* 12–18 mm wide, sterile apex acuminate, 7–9 mm long, with a sharply curved claw-like tip, 5–7 mm long. *Megasporophylls* with 2–8 ovules; sterile part lanceolate, 50–80 × 18 mm, acuminate, marginal teeth numerous, 1–2 mm long, spreading, acumen c. 10 mm long. *Seeds* glaucous when young, 25–37 × 20–27 mm.

Distribution — Australia, scattered and rare along the northern coast of Queensland and the northernmost coast of Western Australia.



Map 3. Distribution of *Cycas lanepolei* C.A. Gardner, *C. normanbyana* F. Muell., *C. furfuracea* W. Fitzg.

Habitat — Open woodland, sometimes on basaltic soils.

Note — The striking laterally spreading teeth on the elongate apical part of the megasporophyll together with sometimes upturned pinnules suggests a relationship with *C. pruinosa*, a near neighbor in Western Australia, while in other ways the resemblance is more with *C. media*, a Queensland neighbor. Some kind of hybrid origin is possible. Hill (1992) reports searching the type areas for examples without success. It may, of course, have disappeared there (Mueller, 1874, in his description said it was rare). Many specimens in Northern Australia lack teeth on the megasporophyll. It appears that insect damage during early development often produces these toothless margins which have been reported in several species in northern Australia.

9. *Cycas furfuracea* W. Fitzg. — Map 3

Cycas furfuracea W. Fitzg., J. & Proc. R. Soc. W Austr. 3 (1918) 108; D.L. Jones, Cycads of the World (1993) 141, photo. — *Cycas media* R. Br. var. *furfuracea* (W. Fitzg.) J. Schust. in Engl., Pflanzenr. 99 (1932) 78. — Lectotype: *Fitzgerald s.n.* (holo NSW), Australia, W Australia, Kimberley Distr.

Cycas arenicola K.D. Hill, Telopea 5 (1993) 419, t. 1 (f. 1b, c, e taken from the type). — Type: *Russell-Smith & Brock 8502* (holo NSW, n.v.), Australia, Northern Territory, Upper E Alligator River.

Trunks at least up to 2 m high, 15–22 cm diam. *Leaves* 60–160 cm long, pinnules 60–140 per side; petiole 14–35 cm long, thorns present in the upper half. *Pinnules* 9–19 × 0.45–0.7 cm, straight to slightly curved towards the apex of the leaf, margin distinctly bent, midrib more prominent below, glossy dark green with a rusty tomentum below. *Pollen cone* narrowly ovoid, 25–38 × 5–9 cm; peduncle c. 5 cm long. *Microsporophylls* 9–20 mm wide, sterile apex acuminate, 12–18 mm long, with a sharply bent tip, 5–12 mm long. *Megasporophylls* with 2–6 ovules; the sterile part triangular, 25–40 × 20–32 mm, acuminate, marginal teeth c. 10 per side, 2–3 mm long, acumen 8–14 (or more) mm long. *Seeds* yellow to orange, glaucous when young, 28–32 × 25–29 mm.

Distribution — Australia, W Australia, Leopold Ranges and Mitchell Plateau, Northern Territory, upper reach of the E Alligator River.

Habitat — Open woodland on sandy soil.

Note — This rare species is more or less intermediate between *C. calcicola* and *C. armstrongii*.

Subgenus *Truncata* de Laub., subg. nov.

Apices microsporophyllorum truncati productionis subulatae inflexus apicalis instructus. Margines apicum megasporophyllorum dentati vel integri, dentes ad 5 mm minusve longes. Foliola 5 mm plusve lata. — Typus: *Cycas rumphii* Miq.

Trunk cylindrical. *Petioles* with or without thorns. *Pinnules* straight or curving towards the base of the leaf, flat or slightly revolute, 5 mm or more wide. *Microsporophylls* truncate (abruptly) narrowed beyond the fertile part so that it becomes more or less peltate, the flat end diamond-shaped with a short to long apical spine emerging from the upper margin nearly perpendicular to the microsporophyll and pointing towards the apex of the cone. Apical part of *megasporophylls* undulate and entire, or, more

often, dentate, teeth more or less obscure basally, more prominent apically, usually much less than 5 mm long, rarely slightly longer, acuminate, acumen often elongated, spike-like.

Distribution — Six species from southern Thailand through the Philippines and Indonesia to New Guinea, Fiji and various Pacific Islands, also outposts in northern Australia.

Habitat — Everwet equatorial regions, mostly in the understory of rain forest; one species in open grassy situations.

Note — The species of this section are all very closely related to one another, differing in minor ways. The majority have a spongy layer inside the stony seed which suggests that the whole subgenus may have had its origin from plants much like *C. thouarsii* but with a truncate rather than an elongated apical part of the microsporophyll. Thus several widespread species retain the strand habitat with buoyant seed while others have moved inland sometimes losing the buoyant seed character. One species, *C. schumanniana*, grows in grasslands within the rain forest zone and resembles in some ways species of the type section. It may have sprung from some kind of genetic interaction with them.

KEY TO THE SPECIES

- 1a. Pinnules usually at least 10 mm wide 2
 b. Pinnules always less than 10 mm wide **15. *C. schumanniana***
 2a. Apical spike of microsporophylls up to 5 mm long. Apical spike of megasporophylls up to 25 mm long. Stony part of the seed with an apical crest 3
 b. Apical spike of microsporophylls at least 12 mm long. Apical spike of megasporophylls at least 25 mm long. Stony part of the seed without an apical crest ... 5
 3a. Pinnules 10–15 mm wide, mostly not acuminate. Apical crest of the seed weak 4
 b. Pinnules 14–18 mm wide, strongly acuminate. Apical crest of the seed prominent **10. *C. rumphii***
 4a. Petiole with numerous thorns. Seed up to 52 × 44 mm ... **11. *C. scratchleyana***
 b. Petiole with few or no thorns. Seed at least 55 × 45 mm **12. *C. celebica***
 5a. Apex of megasporophylls with lateral teeth. Seed not buoyant, up to 45 × 37 mm **13. *C. silvestris***
 b. Apex of megasporophylls toothless. Seed buoyant, at least 55 × 40 mm **14. *C. edentata***

10. *Cycas rumphii* Miq. — Map 4

Cycas rumphii Miq., Bull. Sci. Phys. et Nat. Néerl. 2 (1839) 45; Comm. Phytogr. (1840) 120; Linnaea 17 (1843) 688, p.p.; Tijdschr. Wisk. Natuurk. Wet. 2 (1849) 286, p.p.; Analecta Bot. Indica 2 (1851) 32, p.p.; Linnaea 25 (1852) 589, t. 2, p.p.; Prodr. Cycad. (1861) 7, p.p.; Arch. Néerl. Sci. Exact. & Nat. 3 (1868) 231, p.p.; DC., Prodr. 16, 2 (1868) 257, p.p.; Warb., Monsunia 1 (1900) 181, t. 7f; Stapf, Kew Bull. (1916) 7, p.p.; Ridl., Fl. Malay Penins. 5 (1929) 284; J. Schust. in Engl., Pflanzenr. 99 (1932) 74, p.p.; K.D. Hill, Aust. Syst. Bot. 7 (1994) 549, f. 6. — Type: Rumphius, Herb. Amboin. 1 (1741) 86, t. 22, 23 (*Oliv. calappoides* or '*Sajor calappa*'), Ambon.

Cycas glauca Lam. ex Loudon, Hort. Brit. (1830) 403, nomen.

Cycas glauca Miq., Comm. Phytogr. (1840) 127, nomen; Monogr. Cycad. (1842) 30; Linnaea 17 (1843) 692.

Zamia corsoniana G. Don, Gard. Mag. 18 (1842) 371. — Type: *Corson s.n.* (holo LINN, n.v.).

Cycas bougainvilleana K.D. Hill, Aust. Syst. Bot. 7 (1994) 557, f. 11. — Type: NGF 19739 (*Sayers*) (holo NSW; iso K), Papua New Guinea, Tonalu Harbour.

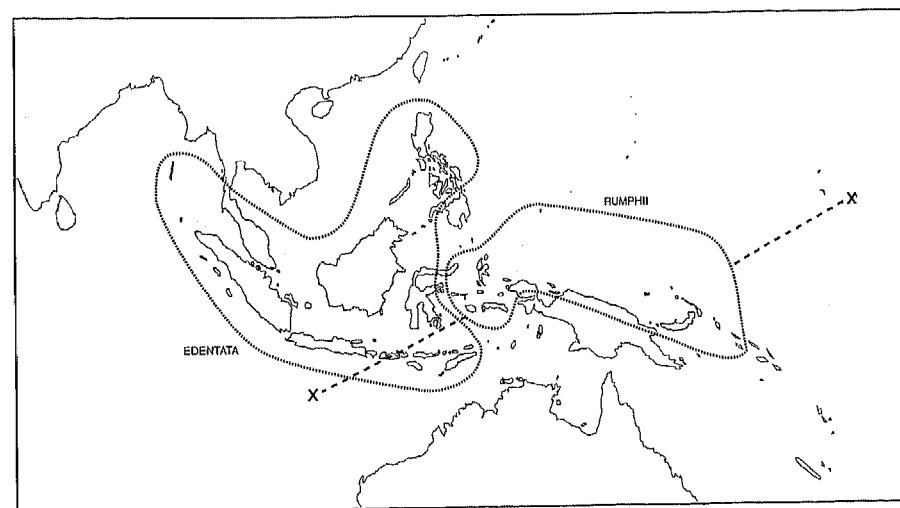
Cycas circinalis auct. non L.: D.L. Jones, Cycads of the World (1993) photos on p. 137.

Trunks up to 12 m high, 20–30(–40) cm diam., often branched. *Leaves* 150–310 cm long, pinnules 95–160 per side; petiole 30–65 cm long, thorns present for most of the length. *Pinnules* 18–30 × (1.2–)1.4–1.8 cm, apex usually distinctly acuminate, margin slightly bent, midrib more prominent below, dark green, shiny above, lighter below. *Pollen cone* ovoid, tapering, 35–45 × 14–20 cm; peduncle up to 13 cm long. *Microsporophylls* 15–20 mm wide, sterile apex with a narrow c. 5 mm long acumen. *Megasporophylls* with 2–10 ovules; the sterile part triangular, 30–45(–60) × 20–30 mm, acuminate, marginal teeth 8–16 per side, 2–3 (lower) to 4–5 (upper) mm long, acumen spine-like, 20–25 mm long. *Seeds* orange, 43–60 × 32–44 mm, apical part of the stony layer with a prominent crest (not visible before the fleshy covering dries), buoyant due to an inner spongy layer.

Distribution — Near the coast. From Sulawesi and the Moluccas, along the northern coast of New Guinea into the Solomon Islands, outposts in the Marshall and Caroline Islands, and on Christmas Island (Indian Ocean).

Habitat — Mostly in strand vegetation in rain forest environments. Although clearly spread locally by flotation, it is known to be spread by people and this probably explains the more remote outposts of its distribution.

Notes — The confusion with other taxa, starting with Miquel himself, has meant that most descriptions of *C. rumphii* are mixed with that of other species or refer to something completely different. The ecology of *C. rumphii* corresponds with that of



Map 4. Distribution of *Cycas rumphii* Miq., *C. edentata* de Laub. The line X-X indicates out-laying collections of *C. rumphii*.

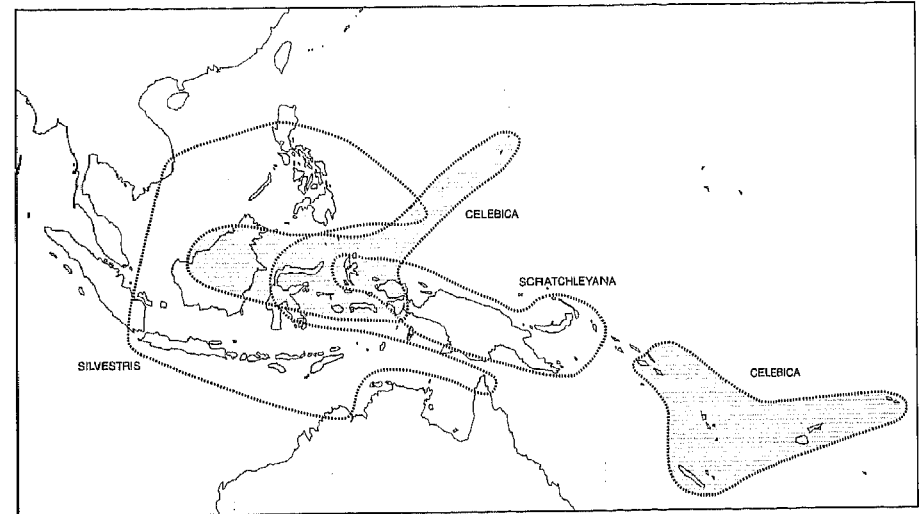
C. thouarsii and *C. edentata*; however, *C. rumphii* can be distinguished by the crested seed, the very short apical spine on the microsporophylls, and the wide, acuminate pinnules. Specimens with pinnules distinctly wider (20–21 mm wide) than in any other *Cycas* species have been collected in Palau. Kanehira (1938: t. 4F, 5F) described a 'forma *palauica*' from there, based on a globular seed with a sharp but low apical ridge. He did not mention the pinnules at all and it remains to be seen if his form has the wide pinnules of *C. rumphii*, and if a distinct taxon is involved. Hill (1994) distinguished *C. bougainvilleana* on the basis of irregular or indistinct lateral teeth (spines) on the apex of the megasporophylls and an interrupted hypodermis in the pinnules. The presence or absence of a small gap in the upper hypodermis in a few samples is probably unreliable as a character and hardly the basis for a species. Hill admits that the teeth are clearly visible in the type (plate 22 of Rumphius which he reproduces) so how he concludes that no more than irregular teeth characterize *C. rumphii* is not clear. In fact, experience with these cycads shows that teeth tend to erode during the time it takes for the seeds to mature. Furthermore, different examples from the same collection show variations in surviving teeth. Thus, three of the four female specimens cited by Hill show clearly developed teeth in the examples examined. Miquel (1840) described *C. glauca* strictly from living plants cultivated at Potsdam and imported by H. Roterod from Java where it undoubtedly also was cultivated. On Java there are no wild plants fitting the description. In fact, no wild plants with a similar shape are known to be glaucous, a factor favored by horticulturalists. The plant described closely resembles *C. rumphii*, which could easily have been carried to Java from Ambon. Without fertile material, which was not available for this taxon to Miquel, not much more can be said. Note that Miquel reported that immature pinnules of *C. glauca* had undulate margins. In 1868 Miquel listed *C. glauca* as of uncertain status in that no wild material known to him was glaucous.

11. *Cycas scratchleyana* F. Muell. — Map 5

Cycas scratchleyana F. Muell., Victorian Naturalist 2 (1885) 18; K.D. Hill, Aust. Syst. Bot. 7 (1994) 562, f. 13. — *Cycas circinalis* L. var. *scratchleyana* (F. Muell.) J. Schust. in Engl., Pflanzenz. 99 (1932) 70. — Type: *Armit s.n.* (holo MEL; iso K), Papua New Guinea, Mt Bedford. *Cycas apoa* K.D. Hill, Aust. Syst. Bot. 7 (1994) 553, f. 9. — Type: *BW 5245 (Iwanggin)* (holo CANB; iso A, L), Irian Jaya, Lake Sentani.

Trunks up to 10 m high, 15–30 cm diam., rarely branched. *Leaves* 150–270 cm long, pinnules 100–160 per side; petiole 33–73 cm long, thorns present for most of the length. *Pinnules* 15–32 × (0.9–)1–1.5 cm, apex sometimes slightly acuminate, shiny dark green above, brighter green below, margin slightly bent, sometimes undulate, midrib more prominent below, sometimes yellow above. *Pollen cone* ovoid, 20–45 (–67) × 10–13 cm; peduncle short. *Microsporophylls* 14–20 mm wide, sterile apex acuminate, acumen narrow, 4–8 mm long. *Megasporophylls* with 4–8 ovules; sterile part triangular, 30–50 × 20–35 mm, acuminate, marginal teeth 14–20 per side, 2–3 (lower) to 4–5 (upper) mm long, acumen spine-like, 5–15 mm long. *Seeds* yellow to yellow-orange, 38–60 × 30–44 mm, apex of the stony layer with a weak crest, buoyant due to a spongy layer under the stony layer.

Distribution — From the Moluccas across New Guinea as far as New Ireland.



Map 5. Distribution of *Cycas scratchleyana* F. Muell., *C. celebica* Miq., *C. silvestris* K.D. Hill.

Habitat — In rain-forest environment, especially along streams. Altitude up to 900 m, occasionally up to 1500 m.

Note — The two species, *C. scratchleyana* and *C. celebica*, form a closely related group with *C. rumphii* with which they share the shape of the microsporophyll, a spongy layer inside the seed, and a crest on the stony part of the seed. In *C. rumphii* the crest is usually more strongly developed, it has also a longer spine at the apex of the megasporophyll, and distinctly wider pinnules. *Cycas scratchleyana* has scarcely acuminate pinnules and somewhat smaller seeds; *C. celebica* has few or no spines on the petiole. *Cycas scratchleyana* appears to be strictly a forest species and less subject to human inter-island transportation even though it is used as human food. The retention of the buoyant seed character clearly illustrates its relationships. Hill (1994) distinguishes *C. apoa* on the basis of irregular or indistinct lateral teeth (spines) on the apical part of the megasporophyll. Two sheets of the type collection seen have well developed teeth (see also the note concerning teeth under *C. rumphii*).

12. *Cycas celebica* Miq. — Map 5

Cycas celebica Miq., Bull. Sci. Phys. et Nat. Néerl. 2 (1839) 45; Comm. Phytogr. (1840) 126; Monogr. Cycad. (1842) 31; Linnaea 17 (1843) 701; Tijdschr. Wisk. Natuurk. Wet. 2 (1849) 288; Prodr. Cycad. (1861) 7; DC., Prodr. 16, 2 (1868) 528. — Type: Rumphius, Herb. Amboin. 1 (1741) 87, t. 20, 21 (*Olus Calappoides*), Sulawesi.

Cycas seemanii A. Braun, Sitzungsber. Ges. Naturf. Fr. Berlin (1876) 268; Carruth., J. Bot. 31 (1893) 2, t. 330; K.D. Hill, Aust. Syst. Bot. 7 (1994) 560, f. 12. — *Cycas circinalis* L. var. *seemannii* (A. Braun) J. Schust. in Engl., Pflanzenz. 99 (1932) 71; A.C. Sm., Flora Viti. Nova 1 (1979) 90. — *Cycas rumphii* Miq. var. *seemannii* (A. Braun) Parham, Agr. J. Dept. Agr. Fiji 19 (1948) 94, f. 7. — Lectotype (Smith 1979): *Seemann 572* (holo K; iso BM, GH, P), Fiji.

Cycas neocaledonica L. Linden, Illust. Hort. 28 (1881) 32, nomen.

Cycas micronesica K.D. Hill, Austr. Syst. Bot. 7 (1994) 554, f. 10. — Type: *Turner s.n.* (holo NSW, photo seen), Guam, Anderson Air Force Base.

Cycas circinalis auct. non L.: Seem., Fl. Viti. (1865) 268; K. Schum. & Lauterb., Fl. Deutsch. Schutzgeb. Südsee (1901) 153; Yunck., Bull. Bishop Mus. 120 (1959) 45; B. C. Stone, Am. Sci. 59 (1951) 313, f. 9; de Laub., Flore Nouv. Caléd. et Dépend. 4 (1972) 8, t. 1; Fosberg & Sachet, Smithsonian Contrib. Bot. 1, 20 (1975) 6.

Trunks up to 15 m high, 14–30 cm diam., often branched. *Leaves* 100–300 cm long, pinnules 65–150 per side; the petiole 25–60 cm long, thorns few or absent. *Pinnules* 15–32 × 1–1.6 cm, when more than 12 mm wide generally distinctly acuminate, margin somewhat bent, midrib more prominent below, green above, paler below. *Pollen cone* ovoid, slightly tapering, 32–60 × 8–15 cm; peduncle c. 7 cm long. *Microsporophylls* 13–18 mm wide, sterile apex acuminate, acumen 4–5 mm long. *Megasporophylls* with (2 or) 4–6 ovules; sterile part triangular or elongated, 35–60 × 25–40 mm, acuminate, marginal teeth 7–14 per side, 2–3 (lower) to 4–5(–7) (upper) mm long, acumen spine-like, 7–30 mm long, occasionally with a few reduced teeth at the base. *Seeds* tawny, 55–70 × 45–60 mm, the apical part of the stony layer with a small crest, buoyant due to an inner spongy layer.

Distribution — Borneo to Moluccas, Bougainville to Tonga, Mariana Islands.

Habitat — In rain-forest environments along the sea coast, also inland. Soil: usually on limestone. Altitude up to 360 m.

Note — Particularly close to *C. rumphii* because of the strand habitat (in part) and the buoyant seed, but differing in the narrower pinnules and thornless petioles. Both Rumphius and Miquel were rather uncertain about the identity of their taxon but emphasized the lack of thorns which certainly distinguishes *C. celebica*. The somewhat disjunct distribution including many islands where the plant is cultivated, suggests, as for *C. rumphii*, that its distribution has been extended by human introductions. Hill (1994), who is content to leave *C. celebica* in the synonymy of *C. rumphii*, supplies *C. micronesica* for the plants from the Marianas, which he distinguishes from *C. seemannii* by an elliptical (rather than triangular) apical part of the megasporophyll and fewer lateral teeth (spines). A wide range of material from the Marianas, New Caledonia, Fiji, and Tonga has been examined and both extremes were found in all four areas. The plants described as *C. circinalis* by Safford (1905) from the Marianas appear to refer to cultivated material of that species as it differs quite sharply from any known wild species collected there.

13. *Cycas silvestris* K.D. Hill — Map 5

Cycas silvestris K.D. Hill, *Telopea* 5 (1992) 181, t. 1 (f. d, e taken from the type). — Type *Clarkson & Neldener 8813* (holo NSW, n.v.), Australia, Queensland, Cook Distr.

Cycas circinalis L. var. *curranii* J. Schust. in Engl., *Pflanzenr.* 99 (1932) 69. — *Cycas spec.*, Foxw., *Philipp. J. Sci., Bot.* 6 (1911) 152, t. 27. — Type *Curran 3842* (holo PNH, destroyed, neo K, here designated; iso P), Philippines, Palawan.

Cycas circinalis auct. non L.: Roxb., *Fl. Ind.* 3 (1832) 744 (excl. pl. Masc.); Blanco, *Fl. Filip.* (1837) 745; Foxw., *Philipp. J. Sci., Bot.* 6 (1911) 151, p.p.; Amoroso, *Philipp. J. Sci.* 115 (1986) 182, t. 5, 7–9, 27–30.

Cycas rumphii auct. non Miq.: Merr., *Sp. Blanc.* (1918) 52; Enum. *Philipp. Flow. Pl.* 1 (1923) 1, p.p.

Cycas media auct. non R. Br.: C.A. Gardner, *For. Dept. Bull. Perth* 32 (1923) 30.

Trunks up to 4.8 m high, 20–25 cm diam. *Leaves* 110–210 cm long, pinnules 70–110 (–120) per side; petiole 24–46 cm long, thorns present at least to halfway above the base. *Pinnules* 17–35 × 0.9–1.5 cm, margin slightly bent, midrib more prominent below, green above, lighter below. *Pollen cone* ovoid, tapering, 28–50 × 8.5–15 cm; peduncle c. 3.5 cm long. *Microsporophylls* 15–22 mm wide, sterile apex with a 12–23 mm long spine, longest towards the centre of the cone. *Megasporophylls* with 4–8 ovules; sterile part triangular, 25–35 × 20–23 mm, acuminate, marginal teeth 7–12 per side, 2–3 (lower) up to 5 (upper) mm long, acumen spine-like, subulate, 25–30 mm long. *Seeds* yellowish, 42–52 × 25–38 mm.

Distribution — From Vietnam through the Philippines to Palau and south to Java and the Lesser Sunda Islands, one or two outposts on the northern coast of Australia.

Habitat — Lowland rain forest, sometimes along the coast.

Note — Hill (1992) described this species from Queensland, well beyond the main area of distribution, based on female material only. The microsporophyll is identical with that of *C. edentata* whose megasporophyll lacks teeth and whose seed has a spongy layer inside the stony layer. Both species and *C. riuminiana* (*C. chamberlainii*) are thoroughly mixed up in the literature and herbaria as in Merrill's 1923 paper or in his collection numbered 855 meant to illustrate Blanco's species. The variety *curranii* was based on a plant with a small pollen cone but this may be no more than the lower limit of the natural size variation.

14. *Cycas edentata* de Laub., *spec. nov.* — Fig. 1, Map 4

Foliola 10–17 mm lata. Productionis apicalis microsporophyllorum 12–24 mm longis. Margines apicum megasporophyllorum edentati integris vel undulates. Semines natan-tes. — Typus: *Kondo & Edaño 38877* (holo L; iso A, BM), Sulu Archipelago, Mt Cabucan.

Cycas rumphii Miq. var. *timorensis* Miq., *Comm. Phytogr.* (1840) 125. — Type: *Serchrusuit s.n.* (holo P), Timor.

Cycas rumphii auct. non Miq.: Dyer in Hook. f., *Fl. Brit. India* 5 (1888) 657; Ridl., *Fl. Malay Penins.* (1925) 186; Smitinand, *Nat. Hist. Bull. Siam Soc.* 24 (1971) 173, t. 3b, 4d, plate 26; *Fl. Thailand* 2, 2 (1972) 186; D.D. Pant, *Cycas and the Cycadales*, ed. 2 (1973) 36, t. 13; Amoroso, *Philipp. J. Sci.* 115 (1986) 182, t. 2, 6, 17–19, 23–26.

Trunks up to 7 m high, 15–30 cm diam., sometimes slightly hypogeal. *Leaves* 100–220 cm long, pinnules 60–108(–120) per side; petiole 45–69 cm long, thorns present for most of the length. *Pinnules* 15–34(–38) × 1–1.8 cm, margin slightly bent, midrib more prominent below, green above, lighter below. *Pollen cone* ovoid, tapering, 30–58 × 11–14 cm; peduncle 4–6 cm long. *Microsporophylls* 14–23 mm wide, sterile apex with a 12–24 mm long spine. *Megasporophylls* with 2–8 ovules; sterile part triangular or almost diamond-shaped, 20–30 × 18–23 mm, acuminate, margin entire, straight or undulating, rarely with a few weak teeth, acumen spine-like, 30–40[–46, Amoroso (1986)] mm long. *Seeds* orange, 55–60 × 40–50 mm, buoyant due to a spongy layer inside the stony layer.

Distribution — From the Andaman Islands through peninsular Thailand and the Philippines south through Indonesia and east as far as Timor.

Habitat — In strand vegetation in rain-forest environments, rarely far from the coast.

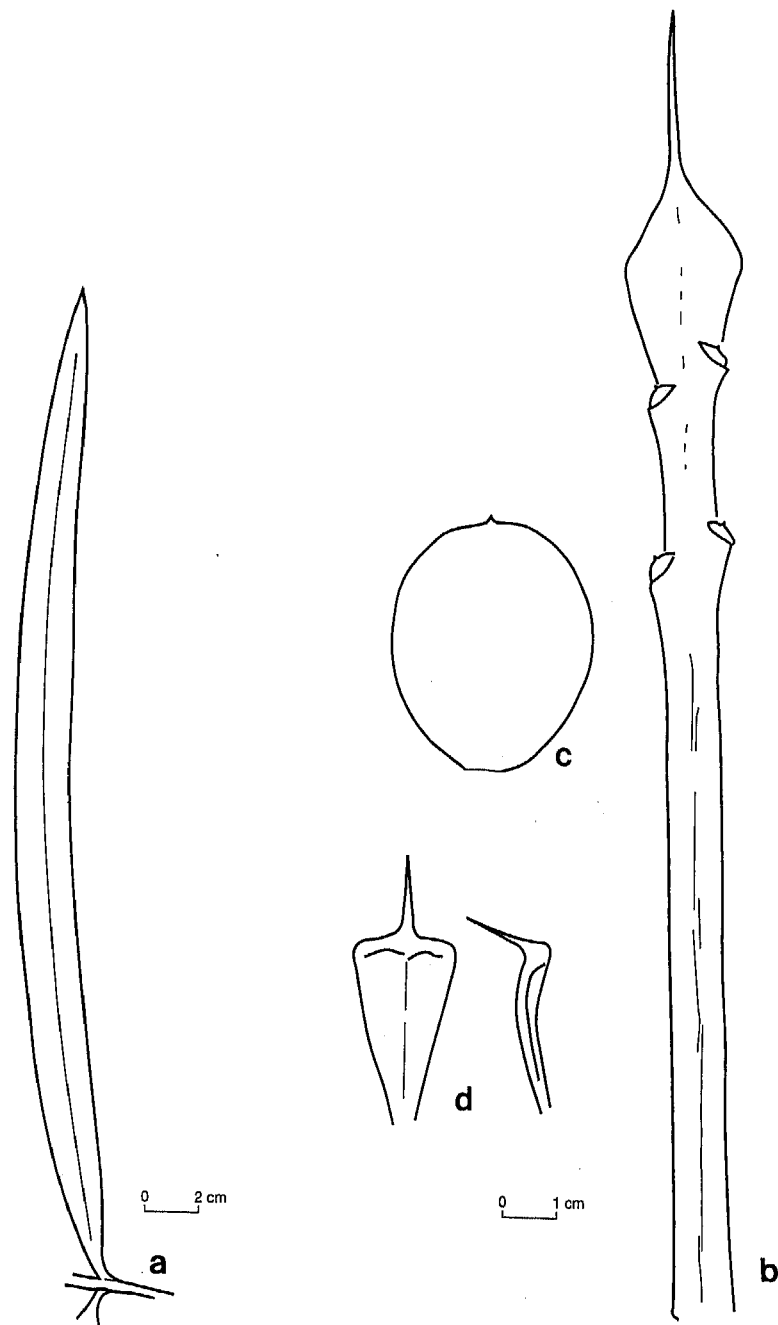


Fig. 1. *Cycas edentata* de Laub. a. Pinnule; b. megasporophyll; c. seed (outline); d. microsporophyll (seen from above and from the side) (a–c: Kondo & Edaño 38877; d: Bartlett 13509).

Note — In spite of the buoyant seeds, its distribution suggests long-distance dispersal by human introduction in part. This species is widely used as a food crop just as its relatives. Sterile plants strongly resemble *C. thouarsii* in shape, albeit somewhat less robust, and in habitat.

15. *Cycas schumanniana* Lauterb. — Map 2

Cycas schumanniana Lauterb. in K. Schum. & Lauterb., Fl. Deutsch. Schutzgeb. Südsee (1901) 154; K.D. Hill, Aust. Syst. Bot. 7 (1994) 536, f. 3B, 8. — Type: Lauterbach 2745 (holo B, destroyed), Papua New Guinea, Bismarck Mts.

Cycas campestris K.D. Hill, Aust. Syst. Bot. 7 (1994) 538, f. 9a–e, g–h, p.p. (all except the type).

Trunks up to 2.5 m high, 20–25 cm diam., occasionally branched. Leaves 75–150 cm long, pinnules 50–105 per side; petiole 24–55 cm long, with several or no thorns. Pinnules 9–22 × 0.5–0.9 cm, margin slightly bent, midrib more prominent below, shiny dark green above, paler below. Pollen cone (probably immature) ovoid, 17–20 × 8–10 cm; peduncle 2.5–4 cm long. Microsporophylls up to 20 mm wide, sterile apex acuminate, acumen c. 3 mm long. Megasporophylls with 2–6 ovules; sterile part triangular, 25–40 × 19–29 mm, acuminate, marginal teeth 10–20 per side, 1–2 (lower) to 2–4 (upper) mm long, acumen 10–15 mm long, usually with a few reduced teeth at the base. Seeds yellow to orange, 28–42 × 23–34 mm.

Distribution — Papua New Guinea, along either side of the major mountain chain.

Habitat — Open grasslands. Altitude up to 1350 m.

Note — Generally identified by collectors as *C. papuana* (*C. armstrongii*) or *C. media*, both of which, however, have microsporophylls with elongated tapering apices with only the tip bent towards the apex of the cone, instead of an obtuse apex with a sharply bent spike. The former has usually narrower pinnules, while the latter usually has longer apices on the megasporophyll. All three species have similar habitats, unlike other New Guinean species that also have wider pinnules and a spike as acumen on the megasporophyll. One could indeed say that *C. schumanniana* is distinctly intermediate between *C. armstrongii* and *C. scratchleyana* and that there is a clear possibility of some sort of hybrid origin. A neotype collected in the Bismarck Mts is needed.

Subgenus *Pectinata* de Laub., *subg. nov.*

Petiolis 25 cm plusve longis. Apicis megasporophyllorum marginalibus pectinatis-laciniatis. Foliolis lineare-lanceolatis, 6–17 mm latis, anguste acutis. — Typus: *Cycas pectinata* Buch.-Ham.

Trunk cylindrical. Petiole more than 25 cm long, usually armed with thorns. Pinnules straight or more commonly turning basally, narrowly acute, flat or slightly bent on the margins, 6–17 mm wide. Microsporophylls with an acute to obtuse apical part, with the apex including the acumen sharply bent towards the apex of the pollen cone. Megasporophylls with a lacinate or pectinate sterile apical part, comb-teeth at least 6 mm long, often more than 1 cm long, usually little variable in size or the middle ones the longest, apex acuminate, acumen narrowly lanceolate to elongated spike-like, usually with few reduced teeth at the base.

Distribution — Seven species from eastern India and southern China through southeastern Asia to the Philippines (Luzon), Indonesia, and New Guinea.

Habitat — Understory or open disturbed areas in rain forest or seasonal forests.

Note — The comb-teeth of the megasporophyll are obviously homologous with foliar pinnules and probably more primitive than the short marginal teeth in the subgenera *Cycas* and *Truncata*, which otherwise strongly resemble this subgenus and could well have been derived from it. Subgenus *Pectinata* more nearly occupies a central (and perhaps ancestral) area for the genus and is more diverse than the other subgenera.

KEY TO THE SPECIES

- 1a. Megasporophyll with more than 10 comb-teeth on each side, the undivided apical part 30–60 × 20–45 mm 2
 b. Megasporophyll with up to 10 comb-teeth on each side, the undivided apical part 20–50 × 15–30 mm 5
 2a. Comb-teeth 12–45 mm long 3
 b. Comb-teeth 6–8 mm long **19. *C. campestris***
 3a. Pinnules 6–9 mm wide. Comb-teeth 12–25 mm long 4
 b. Pinnules 8–12 mm wide. Comb-teeth 20–45 mm long . . . **18. *C. szechuanensis***
 4a. Apex of microsporophylls with a 1–4 mm long spike **16. *C. pectinata***
 b. Apex of microsporophylls with a c. 4 mm long triangular beak
 **17. *C. taiwaniana***
 5a. Apex of megasporophylls triangular, 15–20 × 15–30 mm (not including the acumen) 6
 b. Apex of megasporophylls lanceolate, 30–50 × 16–19 mm (not including the acumen) **20. *C. javana***
 6a. Pinnules 12–17 mm wide **21. *C. macrocarpa***
 b. Pinnules 7–12 mm wide **22. *C. riuminiana***

16. *Cycas pectinata* Buch.-Ham. — Map 6

Cycas pectinata Buch.-Ham., Mem. Wern. Soc. 5, 2 (1825) 322; K.D. Hill, Taxon 44 (1995) 26. — Lectotype (here designated): *Hooker & Thomson s.n.* (K), E Bengal, Chittagong.

Cycas pectinata Griff., Not. Pl. As. 4 (1854) 10, t. 360, f. 3, nom. inval.; Dyer in Hook., Fl. Brit. India 5 (1888) 657; Leandri, Fl. Indo-Chine 5 (1931) 1090; Smitinand, Nat. Hist. Bull. Siam Soc. 24 (1971) 169, f. 3d, 4a; Fl. Thailand 2, 2 (1972) 190, f. 13d, 14a; D.D. Pant, *Cycas* and the Cycadales, ed. 2 (1973) 37; D.L. Jones, *Cycads of the World* (1993) 151. — *Cycas circinalis* L. var. *pectinata* (Griff.) J. Schust. in Engl., Pflanzenr. 99 (1932) 68. — Type: Griffith, Not. Pl. As. 4 (1854) 10, t. 360, f. 3.

Cycas jenkinsiana Griff., Not. Pl. As. 4 (1854) 9, t. 360, f. 1–2, t. 362, f. 1. — Type: *Jenkins s.n.* (holo BM), Assam.

Cycas dilatata Griff., Not. Pl. As. 4 (1854) 15. — No type indicated, see notes.

Cycas siamensis auct. non Miq.: Dyer in Hook., Fl. Brit. India 5 (1888) 657; Ridl., Fl. Malay Penins. 5 (1925) 285; Leandri, Fl. Indo-Chine 5 (1931) 1088, p.p.; Smitinand, Nat. Hist. Bull. Siam Soc. 24 (1971) 173 p.p., f. 3a, 4b; Fl. Thailand 2, 2 (1972) 190 p.p., f. 13a, 14b.

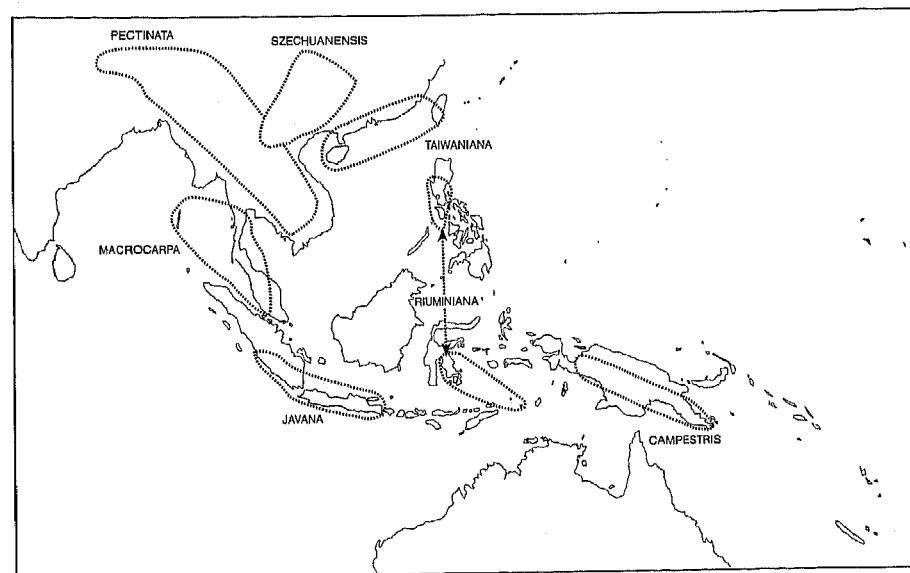
?*Cycas multifida* Chang & Y.C. Zhong, Acta Sci. Nat. Univ. Sunyatsenia 36 (1997) 70, f. 5. — Type: *Y.C. Zhong 80196* (holo SYS, n.v.), China, Guangxi, Xiling.

Trunks up to 8 m high, 14–36 cm diam., sometimes branched. *Leaves* 120–200 cm long, pinnules 80–115(–140) per side; petiole 25–54 cm long, thorns present up to halfway. *Pinnules* 13–25 × 0.6–0.9 cm, margin distinctly bent, midrib prominent, green above, lighter below. *Pollen cone* cylindric, tapering, 35–45 × 11.5–15 cm; peduncle c. 6 cm long. *Microsporophylls* 17–23 mm wide, sterile apex rather abruptly narrowed to an acuminate, sharply upward bent spike, 10–40 mm long, at the base 3–4 mm wide. *Megasporophylls* with 2–6 ovules; sterile part triangular or somewhat rounded, 30–50 × 25–45 mm, acuminate, comb-teeth 12–18 per side, 12–25 mm long, acumen linear to lanceolate, 24–40(–60) mm, usually with a few reduced teeth at the base. *Seeds* yellow to orange, 30–44 × 28–36 mm.

Distribution — From eastern Nepal and the southernmost edge of China across most of SE Asia.

Habitat — In the understory of moist evergreen forest on clay. Altitude mostly above 600 m to 1300 m.

Note — The incomplete notes of Griffith were published posthumously. He certainly did not intend *C. pectinata* Griff. to be a new species as he did not append his name to it, and no specimen can be associated with his figure. Because no reference to Hamilton's species of the same name was included, Griffith's *C. pectinata* becomes a synonym. The species is most often, quite inappropriately, attributed to him. In fact, Griffith described *C. jenkinsiana* which is also a synonym. Further he had obviously laid the name *C. dilatata* aside in favor of *C. jenkinsiana*, that, however, was published anyway, creating yet another synonym. Hamilton cited *C. angulata* with a question mark and further thought his species might be what Rumphius had in mind for *Olus calapoides*, neither of which proved to be correct. Hamilton specified E Bengal as



Map 6. Distribution of *Cycas pectinata* Buch.-Ham., *C. taiwaniana* Carruth., *C. szechuanensis* Chen & Fu, *C. campestris* K.D. Hill, *C. javana* (Miq.) de Laub., *C. macrocarpa* Griff., *C. riuminiana* Porte ex Regel.

locality for his species without a specimen. The early collection by Hooker & Thomson from that area can be taken as the lectotype. Later, *Epicycas siamensis* has been thoroughly confused with *Cycas pectinata* in the literature. Smitinand (1971, 1972), for example, illustrated fertile structures of *C. pectinata* as *C. siamensis* (*Epicycas siamensis*), while Leandri's figures of *C. pectinata* are mostly *Epicycas siamensis*. The new species *C. multifida* differs in the wider pinnules (as in *C. szechuanensis*) and the more numerous comb-teeth, which are not nearly as long as in *C. szechuanensis*. *Cycas multifida* may well stand as a separate species.

17. *Cycas taiwaniana* Carruth. — Map 6

Cycas taiwaniana Carruth., J. Bot. 31 (1893) 2, t. 331. — *Cycas revoluta* Thunb. var. *taiwaniana* (Carruth.) J. Schust. in Engl., Pflanzenr. 99 (1932) 84; K.D. Hill & E.J. Chen, Acta Phytotax. Sin. 32, 6 (1994) 546, f. 6. — Type: *Swinhoe 14119* (holo BM; iso K), Taiwan.
Cycas hainanensis C.J. Chen ex W.C. Cheng, L.K. Fu & C.Y. Cheng, Acta Phytotax. Sin. 13, 4 (1975) 82; S.H. Fu et al., Fl. Reip. Pop. Sin. 7 (1978) 16, f. 2, 5, 6 (taken from the type); D.L. Jones, Cycads of the World (1993) 143; K.D. Hill & C.J. Chen, Acta Phytotax. Sin. 32, 6 (1994) 544, f. 5. — Type: *Zhong 4706* (holo IBSC, n.v.), Hainan.

Trunks up to 3.5 m high, 13–35 cm diam. *Leaves* 65–200 cm long, pinnules 130–170 per side; petiole 20–35 cm long, thorns present for most of the length. *Pinnules* 12–32 × 0.7–1.2 cm, margin flat, midrib prominent above, sometimes weaker below, shiny green above, paler below. *Pollen cone* unknown. *Microsporophylls* c. 17 mm wide, sterile apex turned upwards, abruptly narrowing to a triangular, c. 4 mm long beak. *Megasporophylls* with 2–4 ovules; sterile part triangular or rounded, 35–60 × 25–40 mm, acuminate, comb-teeth 10–24 per side, 20–35 mm long, acumen somewhat longer than the comb-teeth, triangular to lanceolate, with a few reduced teeth or serrations at the base. *Seeds* yellow, 35–45 × 30–36 mm, becoming irregularly rugose, the stony layer verrucose.

Distribution — Hainan, along the nearby coast of China, and apparently formerly on the southwest coast of Taiwan.

Habitat — Scattered in moist forests. Altitude from sea level up to 1200 m. Endangered.

Notes — Long confused with another species from the interior of Taiwan recently named *C. taitungensis*. The authors of this new species argue for an origin of the type material of *C. taiwaniana* on mainland China due to the fact that it is not known today from Taiwan and that Swinhoe did collect extensively on the mainland. Although they quoted evidence from Dyer (1903), they ignored the comments of Watters (who served under Swinhoe), quoted by Dyer, that he had “several conversations about a *Cycas* which grew abundantly on Saracen's Head at the entrance of the harbour. That was in 1865 and since then the Chinese have altered the flora of the place very much by cutting away everything for the erection of a fort and the constructions of roads.” (original in K). This locality is on the southwest coast of Taiwan in an area where Swinhoe is known to have collected. These authors further included material of more than one species in their description of *C. taiwaniana*. Schuster (1932) made Carruth's species a variety of *C. revoluta* based on ‘living’ (cultivated) material which was in fact *C. taitungensis*, a close relative of *C. revoluta*. By contrast, *C. taiwaniana* is very similar to *C. pectinata* which differs in the long apical spike on the microsporophyll

and the smooth, not verrucose surface of the stony layer of the seed. Hill & Chen (1994) distinguish *C. taiwanensis* from *C. hainanensis* by pinnules more than 13 mm wide. However the type of *C. taiwanensis* has pinnules less than 12 mm wide. Apparently Hill & Chen have included material of *C. szechuanensis* in their description of *C. taiwanensis*.

Isolated microsporophylls found in the specimen have been described, the pollen cone itself is still unknown.

18. *Cycas szechuanensis* Chen & Fu — Map 6

Cycas szechuanensis Chen & Fu, Acta Phytotax. Sin. 13 (1975) 81; S.H. Fu et al., Fl. Reip. Pop. Sin. 7 (1978) 12, f. 1: 7–8 (taken from the type). — Type: *Xlong et al. 33221* (holo PE, n.v.), Sichuan.
Cycas guizhouensis Lan & Zou, Acta Phytotax. Sin. 21 (1983) 209, f. 1. — Type: *Lan & Zou 81-8-001* (holo PE, photo seen), Guizhou, Xingyi.
Cycas ferruginea Wei, Guihaia 15 (1994) 300, f. 1–6. — Type: *Wei 1986* (holo IBK, n.v.), cult. Guangxi.
Cycas longlinensis Chang & Y.C. Zhong, Acta Sci. Nat. Univ. Sunyatsenia 36 (1997) 68, f. 8. — Type: *Y.C. Zhong 80848* (holo SYS, n.v.), China, Guanxi, Longlin, Jin Zhong Shan.
Cycas xilingensis Chang & Y.C. Zhong, Acta Sci. Nat. Univ. Sunyatsenia 36 (1997) 69, f. 6, 7. — Type: *Y.C. Zhong 80866* (holo SYS, n.v.), China, Guanxi, Xiling.
Cycas rumphii auct. non Miq.: S.H. Fu et al., Fl. Reip. Pop. Sin. 7 (1978) 16, f. 3: 4, 6–8 (excl. female plants).

Trunks up to 4 m high, up to 30 cm diam. *Leaves* 140–200(–250) cm long, pinnules 70–120 per side; petiole 40–70 cm long, thorns present for most of the length. *Pinnules* 17–29(–35) × 0.8–1.4 cm, margin slightly bent, midrib prominent above, sometimes weaker below, green above, lighter below. *Pollen cone* unknown. *Microsporophylls* c. 12 mm wide, sterile apex turned upwards, abruptly narrowing to a c. 3 mm long, triangular beak. *Megasporophylls* with 2–8 ovules; sterile part triangular or rounded, 40–50 × 20–40 mm, acuminate, comb-teeth 8–19 per side, 20–45 mm long, acumen 30–45 mm long, usually with reduced teeth at the base. *Seeds* yellow, c. 35 × 38 mm (wider than long!).

Distribution — China, from southern Sichuan Prov. to the south coast.

Habitat — In understory of forested areas and grasslands. Altitude up to 1800 m.

Notes — The long comb-teeth resemble those of several species of subgenus *Revoluta* but the pinnules are much broader with a prominent midrib. The megasporophyll of the type appears abnormal with its multiple apex and overlapping seeds and comb-teeth. The type is known from a cultivated plant that exists in clones in several gardens. Without the abnormalities, it is morphologically similar to *C. guizhouensis* which was published later.

Isolated microsporophylls found in the specimen have been described, the pollen cone itself is still unknown.

19. *Cycas campestris* K.D. Hill — Map 6

Cycas campestris K.D. Hill, Aust. Syst. Bot. 7 (1994) 538, f. 3c, 9f (figures taken from the type). — Type: *Jacobs & Conn 5950* (holo NSW, photo seen), Papua New Guinea, Central Prov., Lea Lea Lakes.

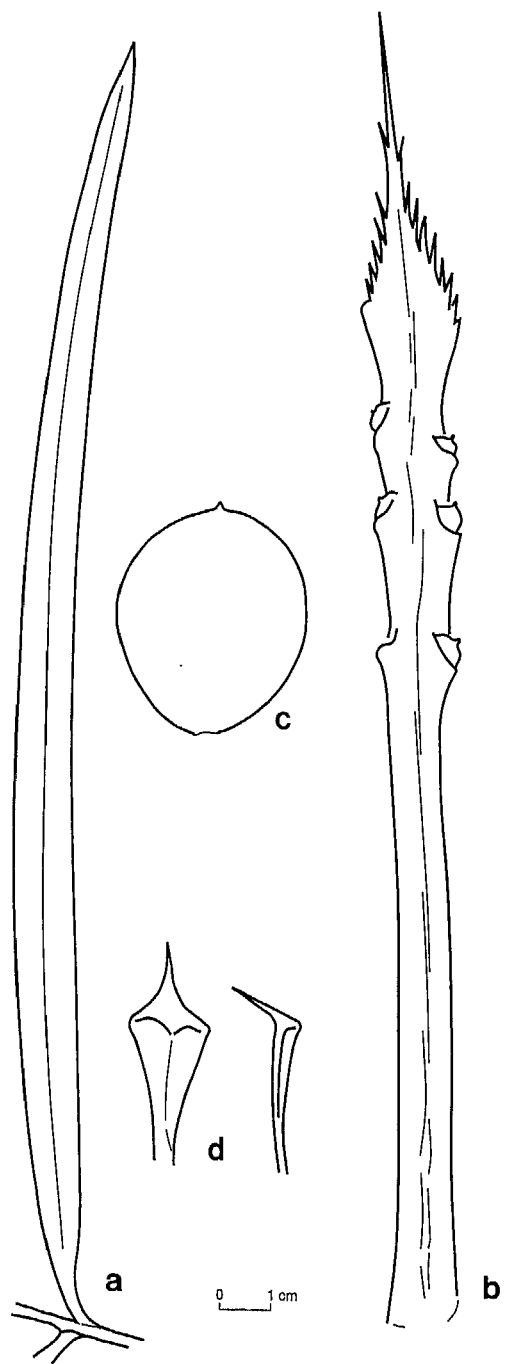


Fig. 2. *Cycas javana* (Miq.) de Laub. a. Pinnule; b. megasporophyll; c. seed (outline); d. microsporophyll (seen from above and from the side) (a, d: *Blume s.n.*; b, c: *Blume 1089*).

Trunks up to 8 m high, 15–30 cm diam. *Leaves* 180–250 cm long, pinnules c. 140 (–180) per side; petiole 33–69 cm long, thorns few to several. *Pinnules* 18–35 × 0.9–1.3 cm, margin distinctly but not strongly bent, midrib prominent, green above, lighter below. *Pollen cone* ovoid, 22 × 5.5 cm; peduncle 2–3 cm long. *Microsporophylls* c. 20 mm wide, sterile apex obtuse, turned upwards. *Megasporophylls* with 4–8 ovules; sterile part triangular, 30–40 × 25–35 mm, acuminate, comb-teeth 8–15 per side, 6–8 mm long, acumen poorly developed, up to 35 mm long, with reduced teeth at the base. *Seeds* red, 38–48 × 30–38 mm.

Distribution — Throughout New Guinea.

Habitat — Scattered in disturbed areas of lowland forest, often along streams. Altitude up to 300 m.

Note — Of the material cited by Hill in the original publication only the type collection belongs to this species, all other material cited represents typical *C. schumanniana*. Both that species and *C. scratchleyana*, which are also found in New Guinea, have shorter teeth on the apical part of the megasporophyll, the teeth are also smaller towards the base, not uniform in size, microsporophylls with distinct apical spikes, while their seeds do not become red. The seed of *C. scratchleyana* has a distinct ridge on the apical part of the stony layer; the pinnules of *C. schumanniana* are much narrower. The relatively short comb-teeth of *C. campestris* are transitional in size between those of subgenus *Pectinata* and those of the subgenera *Cycas* and *Truncata*.

20. *Cycas javana* (Miq.) de Laub., *comb. nov.*, *stat. nov.* — Fig. 2, Map 6

Basionym: *Cycas circinalis* L. var. *javana* Miq., Monogr. Cycad. (1842) 28, t. 2f, E. — Type: *Blume 1089* (holo L), Java.

Cycas rumphii auct. non Miq.: J. Schust. in Engl., Pflanzenz. 99 (1932) 74, f. 11G; Backer & Bakh. f., Fl. Java 1 (1964) 87.

Trunks up to 6 m high. *Leaves* 120–140 cm long, pinnules c. 90 per side (see notes); petiole 45–50 cm long, thorns present for most of the length. *Pinnules* 23–36 × 1.1–1.5 cm, margin slightly bent, midrib prominent, green above, lighter below. *Pollen cone* ovoid, 30–70 × 12–17 cm; peduncle 2–3 cm long. *Microsporophylls* c. 15 mm wide, sterile apex acuminate, extending 5–7 mm and then sharply bent in a 10–15 mm long beak. *Megasporophylls* with 4–8 ovules; sterile part expanding gradually and then lanceolate, 30–50 × 16–19 mm, comb-teeth 6–9 per side, 4–6 (lower) to 6–9 (upper) mm long, apical spike 35–50 mm long, with several reduced teeth at the base. *Seeds* orange, 45–60 × 35–50 mm.

Distribution — South Sumatra, Krakatoa and Java.

Habitat — Understory of lowland rain forest.

Note — Sterile material strongly resembles *C. silvestris* and *C. edentata*, both of which occur in or near Java. The fertile material, however, is quite different. There are only a few specimens known. The fragments of the leaves of these suggest that the leaves may be larger, probably at least up to 200 cm. Of course the number of pinnules should also be larger.

21. *Cycas macrocarpa* Griff. — Map 6

Cycas macrocarpa Griff., Not. Pl. As. 4 (1854) 11, t. 362, f. 11. — Type: *Griffith 6361* (holo K), Malaysia, Crew, near Tabong.

Cycas circinalis auct. non L.: Smitinand, Nat. Hist. Bull. Siam Soc. 24 (1971) 168; Fl. Thailand 2, 2 (1972) 186.

Trunks up to 9 m high, at least 13 cm diam. *Leaves* 100–250 cm long, pinnules c. 120 per side; petiole 40–68 cm long, thorns present up to halfway. *Pinnules* 19–39 × 1.2–1.7 cm, often acuminate, margin flat, midrib prominent. *Pollen cone* cylindric, 33–35 × 7.6 cm; peduncle 2–3 cm long. *Microsporophylls* c. 12 mm wide, sterile apex triangular or acuminate, extending for c. 10 mm, then sharply bent upwards with a 7–8 mm long beak. *Megasporophylls* with 2–8 ovules; sterile part triangular or wedge-shaped, c. 20 × 15–30 mm, obtuse or truncate, abruptly acuminate, comb-teeth 6 or 7 per side, 8–12 mm long, acumen a 25–35 mm long spike. *Seeds* yellow, 50–75 × 35–45 mm.

Distribution — Peninsular Thailand, Peninsular Malaysia.

Habitat — Understory of lowland rain forest often on limestone hillsides.

Note — The forest form mentioned by Ridley (1925: 285) sub *C. rumphii* probably belongs here.

22. *Cycas riuminiana* Porte ex Regel — Map 6

Cycas riuminiana Porte ex Regel, Gartenfl. 12 (1863) 16, f. on p. 17. — *Cycas circinalis* L. subsp. *riuminiana* (Porte) J. Schust. in Engl., Pflanzenr. 99 (1932) 68. — Lectotype (here designated): Regel 6210 (K), cultivated in Manila.

Cycas chamberlainii W.H. Br. & Kienholz, Philipp. J. Sci. 26 (1925) 47, fig. 1, pl. 1–3; Zamora & Co, Guide Philipp. Fl. and Fauna 2 (1986) 219; Amoroso, Philipp. J. Sci. 115 (1986) 181, f. 4, 14–16, 39–41; D.L. Jones, Cycads of the World (1993) 136. — Type: *Brown & Kienholz 42539* (holo US; iso A, BM, K, NY, P), Philippines, Luzon, Mt Arayat.

Trunks up to 8 m high, 15–25 cm diam. *Leaves* 115–220 cm long, pinnules 80–115 (–150) per side; petiole 26–57 cm long, thorns present at least up to halfway. *Pinnules* 18–30 × 0.7–1.2 cm, margin slightly bent, midrib prominent green above, lighter below. *Pollen cone* ovoid, c. 45 × 12 cm; peduncle c. 15 mm long. *Microsporophylls* 16–20 mm wide, sterile apex abruptly rounded, beak lanceolate, 12–20 mm long, spreading but strongly curved upwards. *Megasporophylls* with 4–8 ovules; sterile part ovate, rounded to nearly obtuse, 15–20 × 20–30 mm (wider than long!), comb-teeth 4–10 per side, 8–18 mm long, apical spike 2–4 cm long. *Seeds* yellowish, 39–50 × 29–36 mm.

Distribution — Philippines, Sulawesi, Moluccas.

Habitat — Understory of lowland rain forest, disturbed areas, often on limestone. Altitude up to 1030 m.

Note — *Cycas riuminiana* was described from cultivated material which originated from Manila.

Subgenus *Revoluta* de Laub., subg. nov.

Foliolis linearis vel in partes apicales vers apex folium curvatis, 8 mm minusve lata, revolutis, costa supra immersa, debila vel plana, apicis acutis vel rotundis. Petiolis 40 cm minusve (plerumque 30 cm minusve). Partes apicalis megasporophyllorum laciniates. — Typus: *Cycas revoluta* Thunb.

Cycas L. sect. *Asiorientales* J. Schust. in Engl., Pflanzenr. 99 (1932) 65.

Trunk erect, usually rather short. *Petiole* less than 40 cm long (usually less than 30 cm), with or without thorns. *Pinnules* straight or at least some in the apical part of the leaf curving towards the apex of the leaf, none over 8 mm wide, margins in most species revolute, sometimes extremely so with thickened margins, midrib above usually in a trough, weakly prominent or flat, apex acute, or in narrower pinnules distinctly rounded. *Megasporophylls* with a lacinate, sterile apical part, comb-teeth usually longest in the middle of the sporophyll or, sometimes, all of the same length.

Distribution — Eight species from India to Japan and the Philippines, also in northern Australia, absent from the equatorial zone.

Habitat — Mostly in restricted almost reticulate populations in open forests and savannahs in distinctly seasonal areas.

Note — The narrow and often strongly revolute pinnules with the midrib above flat or only weakly prominent, as well as the short petioles and the tendency of the pinnules to curve towards the apex of the leaf in the parts near the apex of the leaf distinguish this subgenus. The leaf apex shows a strong tendency to have several rapidly diminishing pinnules rather than the more usual one or none. However, this character varies from leaf to leaf and is often absent. In most species of the subgenus the leaves are not flat but rather more or less V-shaped: the two rows of pinnules are raised to form a trough. This character is also variable: in some species often seen, but sometimes hardly noticeable. Short petioles and upward curving pinnules along with pinnule rows forming a trough also characterize several Australian species of subgenus *Cycas*; in that case hybridization with species of subgenus *Revoluta* may have occurred.

KEY TO THE SPECIES

- 1a. Pinnules mostly not more than 4 mm wide, strongly revolute 2
- b. Pinnules 4–8 mm wide, moderately revolute. — Microsporophyll with a short prickle 6
- 2a. Petioles less than 15 cm long. Pinnules distinctly secund, glabrescent 3
- b. Petioles 10–24(–32) cm long. Pinnules not secund, persistently tomentose below. — Pinnules 5–14 cm long 28. *C. calcicola*
- 3a. Microsporophylls with a long apical spike or a claw. Comb-teeth of megasporophylls up to 25 mm long 4
- b. Microsporophylls with a short apical prickle. Comb-teeth of megasporophylls 30–40 mm long 23. *C. revoluta*
- 4a. Apex of microsporophylls narrowing to a projecting spike, the end sharply bent towards the apex of the pollen cone 5
- b. Apex of microsporophylls with a narrow spine curving gradually towards the apex of the pollen cone 27. *C. beddomei*
- 5a. Sterile apex of megasporophylls lanceolate, 11–18 cm long, comb-teeth 10–15 per side 29. *C. pruinosa*
- b. Sterile apex of megasporophylls triangular, 5–7 mm long, comb-teeth 4 or 5 per side 30. *C. cairnsiana*
- 6a. Stony layer of the seed with distinct ribs 7
- b. Stony layer of the seeds not ribbed 26. *C. immersa*
- 7a. Petiole 10–30 mm long. Mature seeds tomentose 24. *C. taitungensis*
- b. Petiole 20–40 cm long. Mature seeds glabrous 25. *C. wadei*

23. *Cycas revoluta* Thunb. — Map 7

Cycas revoluta Thunb., Nova Acta Soc. Sci. Upsal. 4 (1783) 40; Murray, Syst. Veg. ed. 14 (1784) 926; Sm., Trans. Linn. Soc. 6 (1802) 312, t. 29, 30; J. Schust. in Engl., Pflanzenr. 99 (1932) 81, f. 10L, 11A, B; D.D. Pant, Cycas and the Cycadales ed. 2 (1973) 31, t. 7, f. 6–8; S.H. Fu et al., Fl. Reip. Pop. Sin. 7 (1978) 7, t. 1, f. 1–6; D.L. Jones, Cycads of the World (1993) 154, photos p. 154, 155. — Type: *Thunberg s.n.* (holo UPS, n.v.), Japan.

Cycas inermis Lour., Fl. Coch. (1790) 632 (in syn.).

Trunks up to 3 m high, occasionally higher, 15–35 cm diam., often branched. *Leaves* 60–150 cm long, pinnules 100–200 per side, the rows bent to form a trough; petiole 4–10 cm long, thorns usually present for the whole length. *Pinnules* 6–20 × 0.3–0.5 cm, margin strongly revolute, thickened, midrib weakly prominent, more or less in a trough above, dark green above, lighter below. *Pollen cone* cylindrical, tapering towards both ends, 20–40 × 4–6 cm, nearly sessile. *Microsporophylls* 11–17 mm wide, sterile apex rounded and blunt, margin upturned, with a triangular, 5 mm long beak. *Megasporophylls* with 4–6 ovules; sterile part triangular, apex rounded and acuminate, 40–60 × 20–25 mm, comb-teeth 12–20 per side, 30–40 mm long, acumen spike-like, 50–60 mm long, with a few reduced teeth at the base. *Seeds* bright orange to red, 35–39 × 24–28 mm, tomentose.

Distribution — Japan, Ryukyu Islands.

Habitat — Rocky places, often limestone.

Note — Most closely related to *C. taitungensis* which has broader pinnules and a ribbed surface on the stony layer of the seed.

24. *Cycas taitungensis* Shen, K.D. Hill, Tsou & Shen — Map 7

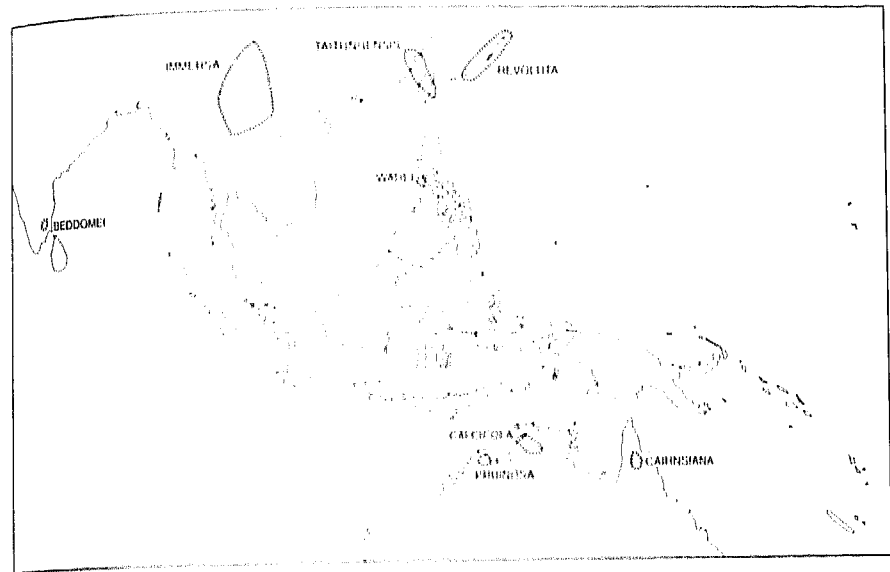
Cycas taitungensis Shen, K.D. Hill, Tsou & Shen, Bot. Bull. Acad. Sci. Sin. 35 (1994) 135, f. 1; K.D. Hill & C.J. Chen, Acta Phytotax. Sin. 32 (1994) 541, f. 3. — Type: *Trou 825* (holo HAST, n.v.), Taiwan, Taitung, Yenping.

Cycas taiwaniana auct. non Carruth.: Yamamoto, Suppl. Ic. Form. 4 (1928) 3, f. 2, t. 1, 2, 4; Kaneh., Formosa Trees, rev. ed. (1936) 30, t. 9; Li & Keng, Taiwaneseana 5 (1954) 27, t. 1; Liu, Ill. Nat. Intro. Lign. Pl. Taiwan 1 (1960) 11, f. 8; Li, Woody Flora Taiwan (1963) 31; Li, Flora Taiwan 1 (1975) 496, t. 170; S.H. Fu et al., Fl. Reip. Pop. Sin. 7 (1978) 9, t. 2, f. 1–4; D.L. Jones, Cycads of the World (1993) 159, photos p. 159, 160. — *Cycas revoluta* Thunb. var. *taiwaniana* (Carruth.) J. Schust. in Engl., Pflanzenr. 99 (1932) 84, p.p., quoad cultivated plants.

Trunks up to 5 m high, 25–45 cm diam., occasionally branched, apex densely tomentose. *Leaves* 100–200 cm long, pinnules 110–200 per side, the two rows bent to form a trough; petiole 10–30 cm long, thorns present for most of the length. *Pinnules* 12–23 × 0.4–0.7 cm, margin nearly flat to somewhat revolute, midrib weakly prominent, more or less in a trough above, dark lustrous green above, lighter below. *Pollen cone* cylindrical, tapering, 30–55 × 8–10 cm; peduncle 2–3 cm long. *Microsporophylls* 14–18 mm wide, sterile apex rounded and obtuse, with a 1–2.5 mm long prickle on the upturned margin. *Megasporophylls* with 2–6 ovules; sterile part triangular to rounded and acuminate, comb-teeth 12–18 per side, 25–40 mm long, acumen up to 20 mm long, with several reduced teeth at the base. *Seeds* orange to bright red, 35–50 × 24–33 mm, tomentose, the stony layer with several longitudinal ribs.

Distribution — Taiwan (interior), China (N Fujian).

Habitat — Disturbed areas in forested zones. Altitude up to 950 m.



Map 7. Distribution of *Cycas revoluta* Thunb., *C. taitungensis* Shen, *C. wadei* Merr., *C. immersa* Craib, *C. beddomei* Dyer, *C. calicicola* Maconochie, *C. pruinosa* Maconochie, *C. cairnsiana* F. Muell.

Note — The tomentose seed, which it shares with *C. revoluta*, a broader acumen on the megasporophyll and a smaller pollen cone are about all that differentiate *C. taitungensis* from *C. wadei* with which it shares the ribbed surface of the stony layer of the seed.

25. *Cycas wadei* Merr. — Map 7

Cycas wadei Merr., Philipp. J. Sci. 60 (1936) 234; Amoroso, Philipp. J. Sci. 115 (1968) 183, f. 1, 20–22, 31–34; Zamora & Co. Guide Philipp. Flora and Fauna 2 (1986) 222, f. 4; D.L. Jones, Cycads of the World (1993) 161. — Type: *Brown s.n.* (holo US; iso GH, K, L, NY), Philippines, Culion Is.

Trunks up to 5.3 m high, 30–40 cm diam., with a swollen base, often branched. *Leaves* 75–132 cm long, pinnules 60–100 per side, the two rows bent to form a trough; petiole 20–40 cm long, thorns present for most of the length. *Pinnules* 14–22 × 0.5–0.8 cm, margin nearly flat to slightly bent, midrib weakly prominent, more or less in a trough above, green above, lighter below. *Pollen cone* cylindrical, tapering, 40–70 × 8–12 cm; peduncle c. 4 cm long. *Microsporophylls* 15–20 mm wide, the sterile apex rounded and obtuse, with a triangular, 5–6 mm long acumen. *Megasporophylls* with 2–4 ovules; sterile part lanceolate to triangular, 50–80 × 25–50 mm, acuminate, comb-teeth 11–14 per side, 20–35 mm long, acumen broad, c. 30 mm long, with a few reduced teeth at the base. *Seeds* 32–40 × 25–30 mm, stony layer with several longitudinal ribs.

Distribution — Philippines, Culion Is., possibly also on Palawan.

Habitat — In grassy, disturbed areas of forested regions.

Note — Yang & Yang (1994, 1996) described material from just north of Vietnam in Yunnan (China) which they called '*Cycas hongheensis*'. These plants resemble *C. immersa*, but differ from that species in precisely the same characters as does *C. wadei*. More information is needed.

26. *Cycas immersa* Craib — Map 7

Cycas immersa Craib, Kew Bull. (1912) 434. — Lectotype (here designated): *Kerr 999* (BM), Thailand, Pang Pua, between Lakon and Phre.

Cycas panzhihuanensis Shou & Yang, Acta Phytotax. Sin. 19 (1981) 335, t. 10, f. 1–6, t. 11, f. 1–10; Zhou, Yang & Zhou, Mem. N. Y. Bot. Gard. 57 (1990) 150; D.L. Jones, Cycads of the World (1993) 150. — Type: *Yang 10* (HP, photo seen).

Cycas baguanheensis G.K. & S.Z. Cheng, Acta Phytotax. Sin. 19 (1981) 337, t. 10, f. 7, t. 11, f. 11–13; D.L. Jones, Cycads of the World (1993) 130. — *Dakou, Yang & Wu 13* (HP, photo seen), China, Sichuan, Baguan He.

Cycas pectinata auct. non Buch.-Ham.: S.H. Fu et al., Fl. Reip. Pop. Sin. 7 (1978) 14, t. 4.

Trunks up to 3.3 m high, 15–25 cm diam., apex densely tomentose. *Leaves* 70–120 cm long, pinnules 50–105 per side, the two rows bent slightly to form a trough; petiole 18–33 cm long, thorns present for most of the length. *Pinnules* 11–23 × 0.5–0.8 cm, margin slightly bent, midrib weak above, dark green above, paler below. *Pollen cone* cylindrical, tapering, 25–46 × 8–11 cm; peduncle c. 5 cm long. *Microsporophylls* 20–28 mm wide, sterile apex obtuse to rounded, with a 3–12 mm long prickly on the upturned edge. *Megasporophylls* with 2–6 ovules; sterile part triangular, 30 × 20–30 mm, rounded to acuminate, comb-teeth 14–20 per side, 20–40 mm long, acumen up to 6 cm long, with reduced teeth at the base. *Seeds* yellow to reddish yellow or orange, 25–30 × 20–25 mm.

Distribution — S China, N Thailand.

Habitat — Open places in broadleaf evergreen forest and sparse-tree-grassland. Altitude up to 2000 m.

Note — The specimen labeled *Kerr 999* at K differs from the sheet at BM and from the description by Craib. The Kew specimen appears to be a misattributed sheet of *Lakshmakara 999* which is *C. siamensis* (see the latter collection at BM). Craib did not specify where his type was deposited. The specimen at K cannot be considered as the type. The outer seed coat (sarcotesta) is frequently shed in this species; however, this also occurs sporadically in many other species.

27. *Cycas beddomei* Dyer — Map 7

Cycas beddomei Dyer, Trans. Linn. Soc., ser. 2, 2 (1883) 85, t. 17; in Hook. f., Fl. Brit. India 5 (1888) 658; D.D. Pant, Cycas and the Cycadales, ed. 2 (1973) 32, f. 9; Rao, Proc. Ind. Acad. Sci. B 79 (1974) 59; D.L. Jones, Cycad of the World (1993) 132. — *Cycas circinalis* L. var. *beddomei* (Dyer) J. Schust. in Engl., Pflanzenz. 99 (1932) 67. — Type: *Yarde s.n.* [holo K; iso BM (with the number 7696)].

Trunks up to 2 m high, 15–35 cm diam., often branched. *Leaves* 90–120 cm long, pinnules at least 100 per side, the two rows bent slightly to form a trough; petiole 10–15 cm long, with few thorns in the upper part. *Pinnules* 9–18 × 0.2–0.4 cm, margin strongly revolute, midrib weak above and more or less in a trough, both sides grey-

green. *Pollen cone* ovate, tapering at both ends, 22–33 × 7.5–9 cm; peduncle 1 cm long. *Microsporophylls* sterile apex c. 15 mm wide, apical margin acuminate, spreading, acumen 8–10 mm long, terminal subulate spike 10–18 mm long, curving upwards. *Megasporophylls* with 2–4 ovules; sterile part lanceolate, c. 40 × 15 mm, acuminate, comb-teeth c. 9 per side, 7–15 mm long, acumen spike-like, 20–40 mm long, with a few reduced teeth at the base. *Seeds* yellow, c. 40 × 37 mm.

Distribution — India, Madras (Cuddapah Hills).

Habitat — Open places in dry deciduous forest.

Note — Geographically far from related species but bearing clear resemblances to both *C. revoluta* of Japan and *C. calcicola* of Australia. The former differs in the fertile material and the color of the pinnules, the latter has rather flat leaves (not secund) and shorter pinnules; there are also other minor differences.

28. *Cycas calcicola* Maconochie — Map 7

Cycas calcicola Maconochie, J. Adelaide Bot. Gard. 1 (1978) 175, f. 1; Krempin, Palms and Cycads around the World (1990) photos p. 20; D.L. Jones, Cycads of the World (1993) 135, photo. — Type: *Maconochie 1314* (holo NT; iso K), Australia, Northern Territory, Katherine.

Trunks up to 3 m high, 17–30 cm diam., not branched. *Leaves* 60–120 cm long, pinnules 75–150(–205) per side, not bent to form a trough; petiole 10–24(–32) cm long, thorns usually present for most of the length. *Pinnules* 5–14 × 0.2–0.5 cm, margin strongly revolute, midrib weak above, more or less in a trough, pubescent below, sometimes silvery pubescent above, especially when new, dark green. *Pollen cone* cylindrical, tapering, 17–26 × 5–7 cm; peduncle unknown. *Microsporophylls* 8–12 mm wide, sterile apex narrowing sharply to a 6–10 mm long beak, the tip sharply curved upwards. *Megasporophylls* with 2–6 ovules; sterile part triangular, 25–30 × 15–20 mm, acuminate, comb-teeth fine papery, 13–18 per side, 2–4 × 1 mm (see note under *C. normanbyana*). *Seeds* orange, glaucous, 28–35 × 25–30 mm.

Distribution — Australia, Northern Territory, S of Darwin.

Habitat — Deciduous woodland, usually on limestone.

Note — Distinguished by the short pubescent pinnules, the flat leaves, and the papery teeth on the megasporophyll. Although the comb-teeth of the megasporophylls of this and the next species are reminiscent of those of the species of subgenera *Cycas* and *Truncata* both species are included here because of the striking similarity in most other characters.

29. *Cycas pruinosa* Maconochie — Map 7

Cycas pruinosa Maconochie, J. Adelaide Bot. Gard. 1 (1978) 177, f. 2; Krempin, Palms and Cycads around the World (1990) photo p. 226, lower left; D.L. Jones, Cycads of the World (1993) 153, photo. — Type: *Symons s.n.* (holo NT; iso K), Australia, Western Australia, Durack Ranges, Teronis Gorge.

Trunks up to 2 m high, 25–40 cm diam. *Leaves* 60–100 cm long; pinnules 60–120 per side, distinctly secund, forming a trough; petiole 4–6 cm long, thorns present for most of the length. *Pinnules* 9–20 × 0.2–0.4 cm, margin strongly revolute, midrib weak above, more or less in a trough, dull grey-green, often glaucous. *Pollen cone* cylindrical,

tapering at both ends, 38–50 × 6–9 cm, nearly sessile. *Microsporophylls* c. 15 mm wide, sterile apex narrowing sharply into a 8–15 mm long beak, this bent slightly towards the base of the cone, its apex sharply hooked upwards. *Megasporophylls* usually with 4 ovules; sterile part lanceolate, 8–11 × 1.2 cm, comb-teeth 10–15 per side, 10–25 × 2–4 mm, terminal spike 3–7 mm long, with a few reduced teeth at the base. *Seeds* (color unknown), glaucous, 35–40 × 30–35 mm.

Distribution — Australia, Western Australia, Kimberley Region.

Habitat — Rocky slopes and ridges in shrubby or grassy areas.

30. *Cycas cairnsiana* F. Muell. — Map 7

Cycas cairnsiana F. Muell., Phragm. Phytogr. Austr. 10 (1876) 63; Krempin, Palms and Cycads around the World (1990) photo p. 226 (labeled in error *C. pruinosa*); K.D. Hill, Telopea 5 (1992) 195, f. 11; D.L. Jones, Cycads of the World (1993) 134, photo p. 136. — Type: *Armit s.n.* (holo MEL; iso BM, K), Australia, Queensland, Newcastle Range.

Trunks up to 5 m high, 12–16 cm diam. *Leaves* 60–110 cm long, pinnules 90–140 per side, distinctly secund; petiole 8–10 cm long, thorns usually present for most of the length. *Pinnules* 8–18 × 0.2–0.4 cm, margin strongly revolute, midrib weak above, more or less in a trough, dull green above, often glaucous. *Pollen cone* cylindrical, tapering at both ends, at least 16–20 × 8–11 cm, nearly sessile. *Microsporophylls* 12–15 mm wide, sterile apex narrowing sharply into an 18–24 mm long beak, the tip sharply bent upwards. *Megasporophylls* with 2–6 ovules; sterile part ovate, c. 40 × 15–20 mm, acuminate, marginal teeth small, 4 or 5 per side, acumen spike-like, 15–24 mm long. *Seeds* (color unknown), glaucous, 36–42 × 30–37 mm.

Distribution — Australia, N Queensland, Newcastle Range.

Habitat — In rocky areas among grass and low shrubs.

Note — The megasporophyll often lacks the lateral teeth (see the discussion under *C. normanbyana*). In most ways this poorly known species resembles *C. pruinosa*, the only clear difference being the much shorter apical part of the megasporophyll. However, if more material becomes available the differences may prove to be less pronounced. Pollen cones known up to now are 16–20 × 8–11 cm. However, comparison with the similar *C. pruinosa* seems to indicate that the pollen cones may be much larger.

EPICYCAS de Laub., *gen. nov.*

Basis in tuborum subterraneum incrassata, caudice gracile fere productis vel apicis foliaribus pluribus. Foliola plana, aliquando dichotoma, basis angustis pedunculatis vel sessilibus. Apices megasporophyllorum laciniati, segmentis aliquando dichotomis. — Typus: *Cycas micholitzii* Dyer [= *Epicycas micholitzii* (Dyer) de Laub.].

Cycas L. sect. *Indosinenses* J. Schust. in Engl., Pflanzenr. 99 (1932) 65. — Type: *Cycas siamensis* Miq.

Cycas L. sect. *Stangerioides* Smitinand, Nat. Hist. Bull. Siam Soc. 24 (1971) 168. — Type: *Cycas micholitzii* Dyer.

Plants with a mostly underground bulbous base, one or more leafy apices on the surface of the bulb, each eventually developing a short, usually slender trunk or underground bulb branched and generally reaching the fertile stage before any trunk forms. *Pinnules*

linear, flat, sessile or with a short petiolule, base sharply narrowed, margin often undulate, dichotomous in some species and then sufficiently dispersed so that adjacent pinnules do not overlap, otherwise spaced as in *Cycas*. Comb-teeth in the apical part of *megasporophylls* often dichotomous, even when the pinnules are not; ovules 1–4 (–10).

Distribution — About eight species from the southern borders of China through SE Asia to northernmost Malaysia.

Habitat — Understory of moist forests or more often in open, disturbed areas.

Note — Most closely related to the genus *Cycas* but differing in the bulbous underground base with relatively slender short trunks or a branching bulb, and, where present, by the dichotomous divisions of the pinnules and comb-teeth. No other cycads of any kind have a combination of a slender stem and a bulbous base. However, bulbs without stems and all kind of subterranean and semi-subterranean stems occur in various genera of other families of cycads. Apart from several species formerly included in *Cycas*, some new species will be described.

KEY TO THE SPECIES

- 1a. Pinnules dispersed, dichotomously divided 2
- b. Pinnules crowded, entire 3
- 2a. Leaves once pinnate. Pinnule segments 20–25 mm wide 1. *E. micholitzii*
- b. Leaves twice pinnate. Pinnule segments 10–25 mm wide .. 2. *E. multipinnata*
- 3a. Pinnules at least 10 mm wide 4
- b. Pinnules up to 10 mm wide 5
- 4a. Trunk short, up to 100 cm long, unbranched. Pinnules at least 13 mm wide. Acumen of megasporophyll almost as long as the comb-teeth 3. *E. tonkinensis*
- b. Trunk longer, several meters long, branched. Pinnules 10–13 mm wide. Acumen of megasporophyll much longer than the comb-teeth 4. *E. spec. nov.* 1
- 5a. Petiole with numerous thorns 6
- b. Petiole with few or no thorns 5. *E. miquelii*
- 6a. Underground bulb unbranched, producing an aerial trunk 7
- b. Underground bulb branched, aerial trunk absent 8. *E. lindstromii*
- 7a. Pinnules 12–24 × 0.6–1 cm. Acumen of megasporophyll at least 25 mm long .
..... 6. *E. elongata*
- b. Pinnules 6–12 × 0.4–0.7 cm. Acumen of megasporophyll up to 25 mm long ..
..... 7. *E. siamensis*

1. *Epicycas micholitzii* (Dyer) de Laub., *comb. nov.* — Map 8

Basionym: *Cycas micholitzii* Dyer, Gard. Chron. 38 (1905) 142, f. 48, 49; Dyer, Fedde Rep. 4 (1907) 171; Prain, Bot. Mag. 135 (1909) t. 8242; Anonymous, Kew Bull. (1910) 163; Anonymous, Kew Bull. (1912) 301, photo on opposite page; Leandri, Fl. Indo-Chine 5 (1931) 1091; J. Schust. in Engl., Pflanzenr. 99 (1932) 81; Smitinand, Nat. Hist. Bull. Siam Soc. 24 (1971) 169, f. 1; D.L. Jones, Cycads of the World (1993) 148. — Type: *Micholitz s.n.* (K), cultivated at Kew.

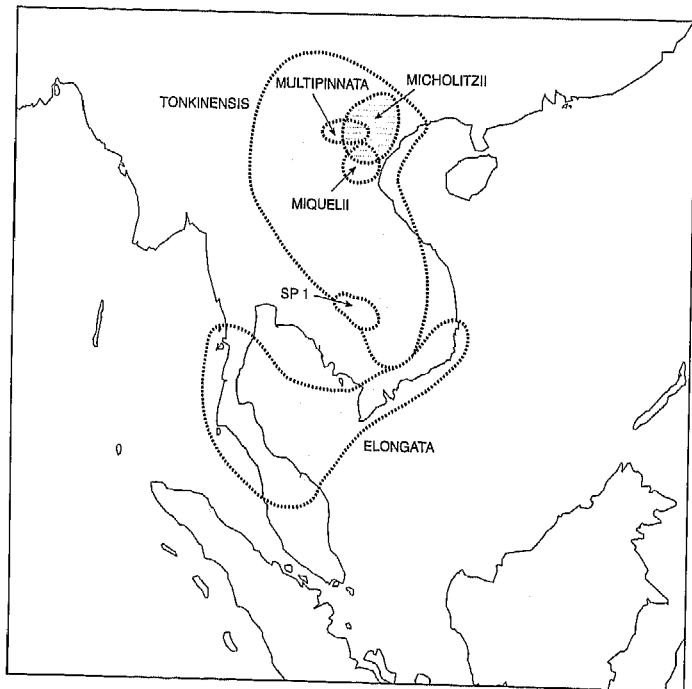
Cycas rumphii Miq. var. *bifida* Dyer, J. Linn. Soc. 26 (1903) 560. — Type: *Morse 273* (K), China, Lungchow.

Bulb subterranean or protruding, c. 30 cm diam. *Trunks* when present up to 45 cm high, 6–12 cm diam. *Leaves* solitary or few, 190–300 cm long, with 10–26 pinnules per side; petiole 60–130 cm, with widely spaced thorns along the whole length; rachis densely tomentose; at the apex several pinnules merging at their bases forming one seemingly terminal, dichotomous pinnule. *Pinnules* dispersed, 4–12 cm apart, 2 or 3 times dichotomous, juvenile and apical pinnules less divided; segments 20–30 × 2–2.5 cm, margins slightly undulate, midrib prominent on both sides, narrowed at the base into a short petiolule (which forms a part of the first dichotomy), apex acuminate, dark green above, paler below, glaucous at first. *Pollen cone* cylindrical, tapering at both ends, up to c. 40 × 6 cm, peduncle c. 12 cm long. *Microsporophylls* c. 17 mm wide, sterile apex ± rounded, acumen short or absent. *Megasporophylls* with 1–4 ovules, sterile part c. 26 × 26 mm, rounded, comb-teeth 5–8 per side, 12–20 mm long, sometimes dichotomous, apex spike-like c. 25 mm long, with 1 or 2 reduced teeth near the base. *Seeds* yellow, at least 20 × 18 mm.

Distribution — S China, NE Vietnam near the Chinese border.

Habitat — Scattered in rain-forest environments.

Note — When the bulbous base protrudes above the ground the trunk looks like a narrow-necked vase.



Map 8. Distribution of *Epicycas micholitzii* (Dyer) de Laub., *E. multipinnata* (Chen & Yang) de Laub., *E. tonkinensis* (L. Linden & Rodigas) de Laub., *E. miquelii* (Warb.) de Laub., *E. spec. nov.* 1 (SP 1), *E. elongata* (Leandri) S.L. Yang.

2. *Epicycas multipinnata* (Chen & Yang) de Laub., *comb. nov.* — Map 8

Basionym: *Cycas multipinnata* Chen & Yang, Acta Phytotax. Sin. 32 (1994) 239. — Type: Yang 9202 (PE, photo seen), China, Yunnan, S Jianshui Co.

Cycas longipetiolula D.Y. Wang in F.X. Wang et al., Cycads in China (1996) 68, pl. 11, f. 6. — Type: Wang & Peng 5523 (SZG, n.v.), China, Yunnan, Pingbian, Yuanjiang river valley.

Bulb subterranean or protruding, 10–25 cm diam. *Trunks* when present up to 40 cm high, c. 3 cm diam. *Leaves* 1 or 2 at a time, up to 700 cm long, twice pinnate, primary pinnae 6–11 per side, middle pinnae up to 90 cm long, upper and lower pinnae 25–90 cm long, longer pinnae with 7–11 dispersed pinnules, apex with several pinnules merging at their bases rather like a single dichotomous pinnule; petiole 80–400 cm long, with thorns along the whole length. *Pinnules* 20–40 cm long, asymmetrically 2 or 3 times dichotomous, apical ones less divided; segments 8–12 × 1–2.5 cm, margin undulate, midrib prominent on both sides, narrowed at the base into a short petiolule (which forms a part of the first dichotomy), apex acuminate, color unknown. *Pollen cone* cylindrical, tapering at both ends, 25–35 × 8–10 cm, peduncle unknown. *Microsporophylls* 8–15 mm wide, sterile apex acute. *Megasporophylls* with 6–10 ovules, sterile part ovate triangular, 50–70 × 45–65 mm, comb teeth 6–9 per side, 20–35 mm long, apex spike-like 30–50 mm long. *Seeds* yellowish brown, 25–32 × 23–28 mm, stony layer finely verrucose.

Distribution — China, S Yunnan near the border with Vietnam

Habitat — Somewhat open forest on limestone.

Note — Cultivated material was studied.

3. *Epicycas tonkinensis* (L. Linden & Rodigas) de Laub., *comb. nov.* — Map 8

Basionym: *Zamia tonkinensis* L. Linden & Rodigas, Ill. Hort. 32 (1885) 27, t. 547. — *Cycas tonkinensis* (L. Linden & Rodigas) L. Linden & Rodigas, Ill. Hort. 33 (1886) 27. — Type: *Zamia tonkinensis* L. Linden & Rodigas, Ill. Hort. 32 (1885) 27, t. 547.

Cycas bellefontii L. Linden & Rodigas, Ill. Hort. 33 (1886) 27, t. 586. — Type: Ill. Hort. 33 (1886) 27, t. 586.

Cycas balansae Warb., Monsunia 1 (1900) 179. — *Cycas siamensis* Miq. subsp. *balansae* (Warb.) J. Schust. in Engl., Pflanzenr. 99 (1932) 1092. — Type: *Balansa 4084* (holo P; iso K), Tonkin, near Hanoi.

Cycas chevalieri Leandri, Fl. Indo-Chine 5 (1931) 1092. — Type: *Fleury 32612* (P), N Annam, Nghe-An Prov.

Cycas micholitzii Dyer var. *simplicipinna* Smitinand, Nat. Hist. Bull. Siam Soc. 24 (1971) 164, f. 2, 3e, 4f; Fl. Thailand 2, 2 (1972) 192, f. 13e, 14f, 15; D.L. Jones, Cycads of the World (1993) 149. — Lectotype (here designated): *Smitinand 4757* (BFK, n.v., f. 2a, b taken from the type), N Thailand, Doi Suthep.

Cycas shiwandashanica Chang & Y.C. Zhong, Act. Sci. Nat. Univ. Sunyatsenia 36 (1997) 67, f. 1–4. — Type: *Y.C. Zhong 88015* (holo SYS, n.v.), China, Guanxi, Fangcheng, Shiwanda Shan.

Bulb subterranean or protruding, up to c. 30 cm diam. *Trunks* when present up to almost 100 cm high, c. 10 cm diam. *Leaves* few, 75–190 cm long, with 18–30 pinnules per side; petiole 25–77 cm, with thorns for most of the length. *Pinnules* not dichotomous, crowded, 17–39 × 1.3–2.5 cm, margin sometimes undulate, midrib prominent on both sides, narrowed at the base into a short petiolule or sessile, apex weakly to distinctly acuminate, glaucous at first, bright green. *Pollen cone* cylindrical, tapering

at both ends, c. 29 × 4–7 cm, peduncle 3–5 cm long. *Microsporophylls* c. 17 mm wide, sterile apex ± rounded, margin turned upwards, acumen small but distinct. *Megasporophylls* with 1–4(–6) ovules, sterile part c. 35 × 15 mm, ovate, comb-teeth 6–12 per side, 20–30 mm long, often dichotomous, apex spike-like 20–40 mm long, sometimes with reduced teeth at the base. *Seeds* yellow, 25–27 × 20 mm.

Distribution — From S China and N Thailand south throughout Vietnam.

Habitat — Understory of lowland rain forest.

Notes — The original description of *Zamia tonkinensis* and *Cycas bellefontii* were made from young plants shipped from Tonkin. The authors distinguished the first by undulate pinnule margins from the latter. The illustration of *Zamia tonkinensis* shows a barrel-shaped base narrowed below. It is almost certain that this was originally mostly underground, a bulbous base which is commonly associated with leaves with this kind of pinnules. In fact, the pinnules of *Zamia tonkinensis* are given as (not very precisely) 2–3 cm wide, a little large for the species that generally has the pinnules up to 25 mm wide. The measurement of the original description were probably a bit exaggerated. It is not unusual for wider pinnules in this species to be undulate. The growth form and wide pinnules resemble *E. micholitzii*; however, the dichotomy of the pinnules is lacking.

Yang & Yang (1994) described material from the same area which they called '*Cycas parvulus*' because of the smaller fruits (without a Latin description or a type). These plants have a verrucose surface of the stony layer of the seed.

4. *Epicycas spec. nov. 1* — Map 8

[*Cycas inermis* Lour., Fl. Coch. (1790) 632, nom. illeg. (given in synonymy with *Cycas revoluta* Thunb.). — *Cycas revoluta* Thunb. var. *inermis* (Lour.) Miq., Prodr. Cycad. (1861) 16. — *Cycas siamensis* Miq. subsp. *inermis* (Lour.) J. Schust. in Engl., Pflanzenr. 99 (1932) 80.]
[*Cycas* sp. 'Saraburi' (K.D. Hill & S.L. Yang, in preparation). See Yang & Meerow (1996) 468.]

Bulb subterranean or slightly protruding, up to 1 m diam. *Trunks* when present several meters high, c. 9 cm diam., often branched, apex densely tomentose. *Leaves* c. 100 cm long, with 74–83 pinnules per side; petiole 24–27 cm, with few or no thorns; at the apex few pinnules united at their bases. *Pinnules* 15–24 × 1–1.3 cm, margins flat, midrib prominent on both sides, narrowed at the base except towards the apex of the leaf, green on both sides. Reproductive material unknown.

Distribution — S Central Thailand, near Saraburi.

Habitat — On limestone at moderate elevation.

Note — The somewhat unusual leaf apex resembles that of *Epicycas multipinnata* and *E. micholitzii*; the pinnules are narrow as in *E. multipinnata* but lacking the dichotomy. The bulb with multiple arial stems is also unusual. Although *Cycas inermis* is not a legitimate name, the description and the locality fit this unnamed species. A Loureiro specimen in BM is labelled as the 'type' of *Cycas inermis* (and therefore for the variety and the subspecies). This specimen has pinnules 32 cm long while Loureiro specified 15 cm for his species. If the variety (subspecies) is validly published and the Loureiro specimen in BM is taken as the type, it does not belong to *Epicycas spec. nov. 1*, but rather to *E. tonkinensis*. *Cycas inermis* (nom. inval.) has been included here because of its description that is similar to that of *Epicycas spec. nov. 1*.

5. *Epicycas miquelii* (Warb.) de Laub., *comb. nov.* — Map 8

Basionym: *Cycas miquelii* Warb., Monsunia 1 (1900) 179. — Neotype: *Kerr 11873* (holo K), S Thailand, K. Yako, Champhon.

Bulb subterranean or slightly protruding. *Trunks* when present up to 100 cm high, slender. *Leaves* less than 100 cm long; petiole 23–39 cm long, with few or no thorns. *Pinnules* 18–30 × 0.6–1 cm, margins slightly bent, sometimes undulate, midrib prominent on both sides, dark green. *Pollen cone* ovoid, c. 63 × 15 cm, peduncle unknown. *Microsporophylls* c. 12 mm wide, sterile apex ± rounded, sharply narrowed with a c. 10 mm long apical spur on the upturned margin. *Megasporophylls* with 4 ovules, sterile part triangular, c. 45 × 40 mm, acuminate, comb-teeth 14–16 per side, up to 20 mm long, acumen up to 40 mm long, with few reduced teeth at the base. *Seeds* yellow, 18–20 × 18–20 mm.

Distribution — Southern China, Vietnam (along the coast). Possibly also in Peninsular Thailand.

Habitat — Limestone on low elevation.

Note — The original type, *Warburg s.n.*, has been destroyed in the Berlin fire. *Kerr 11873* has been chosen as the neotype. The species resembles the previous one but has narrower pinnules. Its relationship with various undescribed species needs further study.

6. *Epicycas elongata* (Leandri) S.L. Yang, *comb. nov.* — Map 8

Basionym: *Cycas pectinata* Griff. var. *elongata* Leandri, Fl. Indo-Chine 5 (1931) 1091. — Type: *Poilane 9328* (holo P), Annam, Ca Na.

Bulb subterranean or slightly protruding, c. 1 m diam. *Trunks* when present up to 6 m high, c. 15 cm diam. *Leaves* 90–130 cm long, with 51–92 pinnules per side; petiole 23–51 cm, with thorns up to halfway. *Pinnules* 12–24 × 0.6–1 cm, margins slightly bent, midrib prominent on both sides, green. *Pollen cone* mostly unknown, c. 11.5 cm diam. *Microsporophylls* c. 18 mm wide, sterile apex triangular, acumen upturned. *Megasporophylls* with 1–4 ovules, sterile part triangular, 30 × 20–30 mm, acuminate, comb-teeth 8–16 per side, 20–30 mm long, acumen 30–60 mm long, usually with a few reduced teeth at the base. *Seeds* yellow, 34–45 × 28–35 mm.

Distribution — From C Vietnam through Peninsular Thailand to northern Malaysia; mostly near the coast.

Habitat — In disturbed and rocky places. Usually on limestone. Alt. up to 500 m.

Note — Superficially similar to *Cycas pectinata* but distinguished by the narrow elongated megasporophyll and, especially, by the bulbous base of the trunk. The populations of Thailand and Malaysia may be different from those of Vietnam; however, no obvious morphological differences have been detected.

7. *Epicycas siamensis* (Miq.) de Laub., *comb. nov.* — Map 9

Basionym: *Cycas siamensis* Miq., Bot. Zeit. 21 (1863) 334; DC., Prodr. 16, 2 (1868) 528; Leandri, Fl. Indo-Chine 5 (1931) 1088, p.p.; J. Schust. in Engl., Pflanzenr. 99 (1932) 80; Smitinand, Nat. Hist. Bull. Siam Soc. 24 (1971) 169, p.p., t. 27; Fl. Thailand 2, 2 (1972) 189, p.p.; Krempin, Palms and Cycads around the World (1990) 228, photo lower left; D.L. Jones, Cycads of the World (1993) 157, p.p. — Type *Teijsmann s.n.* (holo U; iso L), Thailand, Kan-Boerle.

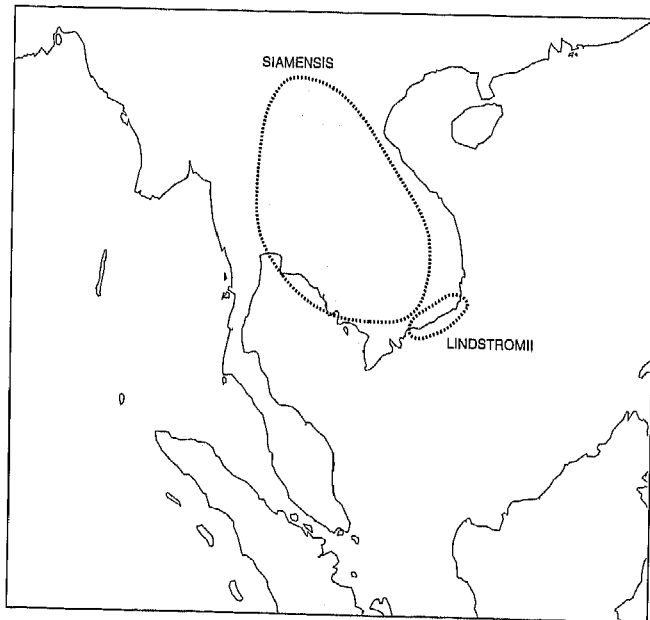
Cycas pectinata auct. non Buch.-Ham.: Leandri, Fl. Indo-Chine 5 (1931) 1090, f. 121, 3–5, 122, 1, 3, 4.

Bulb subterranean or protruding, c. 1 m diam. *Trunks* when present up to 2.5 m high, 8–20 cm diam. *Leaves* 45–110 cm long, with 50–103 pinnules per side; petiole 8–18 cm, usually with thorns along the whole length, sometimes thornless, rachis pubescent when young. *Pinnules* 6–12 × 0.4–0.7 cm, margins flat, midrib prominent on both sides, apex acute to rounded, green, paler below. *Pollen cone* cylindrical or oblong, 20–30 × 6–8 cm, peduncle 1–2 cm long. *Microsporophylls* 17–20 mm wide, sterile apex acuminate, 7–12 mm long, with a sharply upturned, 5–10 mm long apical hook. *Megasporophylls* with 2–4 ovules, sterile part triangular, 22–35 × 17–30 mm, acuminate, comb-teeth c. 10 per side, 6–10 mm long, acumen spike-like 14–25 mm long, with several reduced teeth near the base. *Seeds* yellow, 29–35 × 30–35 mm.

Distribution — From Myanmar across most of Thailand into southern Vietnam.

Habitat — Dry deciduous forest on poor soil. Altitude up to 1200 m.

Note — The small pinnules and short petiole of this and the next species differ sharply from those of the other species. However, they retain the flatness typical for the genus. There is some overlap in leaf morphology with *Cycas pectinata* which has led to some confusion (see discussion under *Cycas pectinata*) in spite of substantial differences. The shorter pinnules of *Epicycas siamensis* have mostly a rounded apex, the microsporophyll is more elongate, the pollen cone cylindrical, and the teeth on the megasporophyll are much shorter, while the stem base is bulbous. Bifurcate pinnules occur sporadically in *Larsen 8102*.



Map 9. Distribution of *Epicycas siamensis* (Miq.) de Laub. and *E. lindstromii* (S.L. Yang, K.D. Hill & Hiep) de Laub.

8. *Epicycas lindstromii* (S.L. Yang, K.D. Hill & Hiep) de Laub., *comb. nov.* — Map 9

Basionym: *Cycas lindstromii* S.L. Yang, K.D. Hill & Hiep, *Novon* 7 (1997) 213. — Type: S.L. Yang 557 (holo FIG; iso NSW, S), Vietnam, Binh Thuan, Tuy Phong, Xa Chi Cong, near Doc Bao Da.

Bulb subterranean often branched, 13–25 cm diam. *Trunks* absent. *Leaves* sometimes few in a whorl, 50–78 cm long, with 18–60 pinnules per side; petiole 6–15 cm, with thorns at least up to halfway. *Pinnules* 10–13 × 0.7–1 cm, diminishing towards the apex of the leaf, margins flat, midrib prominent, dark green above, paler below. *Pollen cone* cylindrical, 16–20 × 4–5 cm, peduncle c. 3 cm long. *Microsporophylls* 11–15 mm wide, sterile apex triangular, c. 6 mm long, slightly rounded, with a sharply upturned 2–8 mm long apical spine. *Megasporophylls* with 2 ovules, the sterile part ovate, c. 60 × 20 mm, acuminate, comb-teeth 6–13 per side, 8–12 mm long, acumen c. 30 mm long, with a few reduced teeth at the base. *Seeds* reddish orange, 31–35 × 20–30 mm.

Distribution — East coast of southern Vietnam.

Habitat — Sandy grassland and open woodland at low elevation.

Note — Differs from *E. siamensis* in the branching bulbs which never form an arial trunk, the narrower megasporophylls, and the shorter leaves.

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IDENTIFICATION LIST

Cycas

- | | | |
|--------------------------|--------------------------|-------------------------|
| 1. <i>circinalis</i> | 14. <i>edentata</i> | 27. <i>beddomei</i> |
| 2. <i>sphaerica</i> | 15. <i>schumanniana</i> | 28. <i>calpicola</i> |
| 3. <i>thouarsii</i> | 16. <i>pectinata</i> | 29. <i>pruinosa</i> |
| 4. <i>media</i> | 17. <i>taiwaniana</i> | 30. <i>cairnsiana</i> |
| 5. <i>armstrongii</i> | 18. <i>szechuanensis</i> | <i>Epicycas</i> |
| 6. <i>angulata</i> | 19. <i>campestris</i> | 31. <i>micholitzii</i> |
| 7. <i>lanepoollei</i> | 20. <i>javana</i> | 32. <i>multipinnata</i> |
| 8. <i>normanbyana</i> | 21. <i>macrocarpa</i> | 33. <i>tonkinensis</i> |
| 9. <i>furfuracea</i> | 22. <i>riuminiana</i> | 34. <i>spec. nov. 1</i> |
| 10. <i>rumphii</i> | 23. <i>revoluta</i> | 35. <i>miquellii</i> |
| 11. <i>scratchleyana</i> | 24. <i>taiungensis</i> | 36. <i>elongata</i> |
| 12. <i>celebica</i> | 25. <i>wadei</i> | 37. <i>siamensis</i> |
| 13. <i>silvestris</i> | 26. <i>immersa</i> | 38. <i>lindstromii</i> |

- Abbe & Smitinand 9361A–B: 16; 9473: 33; 9573: 36 — Aet 704: 12 — Anderson 3719: 10 — Armstrong 379: 5; 380: 5 — Aston S17927: 12 — Atasrip 60: 10.
- Backer 50: 13; 1476: 20; 27471: 14; 37088: 20 — Baker 199: 12; 301: 12 — Balansa 563: 33; 4084: 33 — van Balgooy 3930: 22 — Barclay 3540: 10 — Baron 2163: 3 — Bartlett 13509: 13 — Baumann 13896: 12 — Beck 108: 3 — Benson GC50: 3 — Bernier 12029: 12 — Berry 79: 10 — van Beusekom et al. 4067: 37 — Blake 16330: 5 — Blume 1089: 20 — Boivin 2891: 3 — Bon 2706 (= 4146): 33 — van Borssum Waalkes 523: 13 — Brass 877: 15; 994: 11; 2852: 12; 5643: 11; 6541: 5; 6752: 11; 18924: 8; 23830: 19 — Brown 3106 p.p.: 4; 3106 p.p.: 6 — Brown & Kienholz 42539: 22 — Bryan 1240: 12 — BSIP series 1347 (Whitmore): 10; 3932 (Whitmore): 10; 9635 (Sirate'e): 12; 197956 (Yen): 10 — Burck 1904: 20 — Buwalda 4622: 22 — Buysman 16: 14 — BW series 5243 (Iwanggin): 11 — Byrnes 2406: 4; 2408: 6; 2465: 5; 2606: 4; 2782: 6.
- Cabiling 3707: 14 — Cardona 23870: 13 — de Carey 5219: 3; 6524: 3 — Carow 25: 23 — Carr 11236: 15; 11555: 15 — Carroll 80: 10 — Cavalerie 7106: 33 — Cavalerie & Fortunat 2001: 26 — Charoenphol et al. 4064: 14 — Chevalier 37888: 31; 40474: 37; 40601: 37 — Ching 2260: 23 — Clemens 751: 11; 1277: 11; 3972: 13; 8104: 11; 10751: 15; 11277: 12; 11369: 15; 21175: 12 — Condomines 16: 31 — Congdon 42: 14 — Conklin 37914: 14 — Corner 30294: 21 — Craven 3211: 4; 4155: 6 — Craven & Schodde 750: 11; 933: 11 — Cunningham 286: 6 — Curran 3842: 13; 7381: 13; 7513: 13; 10319: 14 — Curtis 2424: 36; 2427: 36.
- Darbyshire 662: 15; 907: 11 — Darbyshire & Hoogland 7855: 10 — Davy 22603: 3 — Degener 15233: 12; 15262: 12; 15286: 12 — Degener & Ordenez 14262: 12 — Dickason 7226: 16; 7623: 16 — Docters van Leeuwen 1531: 10; 9623: 11; 1881: 13 — Dunlop 2955: 5; 2955C: 6 — Dunlop & Byrnes 2156: 28.
- Edaño 76373: 13 — Erlanson 5398: 1 — Evans 2148/9: 12 — Everist 7612: 6 — Eyma 3727: 13; 5451: 19.
- Faden 74/317: 3 — Fell 1798: 6 — Fenix 15660: 14 — Fernando 7181: 14 — Field 2960: 21 — Field & Low 105: 23 — Fischer 2613: 1 — Fleury 326122: 33 — Floyd 6423: 11 — Forman 176: 14 — Fosberg 25300: 12; 26192: 10; 31830: 12; 32009: 10; 32644: 12; 36632: 10; 37634: 23; 37935: 23; 38242: 23; 46237: 10; 46256: 12; 32376: 13 — Fosberg & Evans 46228: 12; 46237: 12 — Fosberg & Sachet 53148: 2 — Foster RLP 78-37: 12 — FRI series 4232 (Whitmore): 21; 5581 (Ng): 21; 7565 (Cockburn): 14; 12993 (Whitmore): 36; 93185 (Wyatt-Smith): 14; 94932 (Meyer & Yong): 21 — Fryxell & Craven 4252: 6.
- Gamble 73 (Robertson): 37; 325B: 16; 2675A: 16; 13668: 1; 14597: 1; 17052: 1; 21278: 27 — Geay 7616: 3 — Geesink & Phengklai 6157: 16 — Gentry 11341: 3 — Gibbs 4337: 14; 6278: 10 — Greenway 1686: 1; 9635: 3 — Greenwood 644: 12 — Gressitt 21: 12; 21: 13 — Grierson & Long 2357: 16 — Griffith 88: 1; 6361: 21 — Guam Experiment Sta. 406: 12 — Guppy 133: 12; 356: 10.
- de Haan 1798: 11 — Haines 3983: 16; 4033: 2; 5876: 2; 5877: 2 — Hallé RSNH 6362/3: 12 — Hansen et al. 31181: 26 — Henderson 20338: 14; 23826 (SFN): 36; 29160: 14 — Hennipman 6113: 22 — Henry 12637: 16; 13637: 26 — Herold 489: 1 — Herre 1061: 25 — Higgins 16597: 27 — Hill & Stanberg 3738: 6 — Hinz A42-73: 6 — Hodel et al. 514: 12; 551: 12 — Hoogerwerf 235: 14 — Hoogland 4750: 19; 5120: 15; 8548: 4 — Hooker & Thomson 10: 1; 11: 1; 595: 16 — Horne 309: 12; 316: 12 — Horsfield 80: 20 — Hosseus 361: 37 — Hu 7059: 18 — Hürlimann 272: 12 — Hutchinson 3441: 14.
- Iboet 237: 14 — Isaac EA 1329: 3.
- Jaag 667: 13; 893: 13 — Jacobs 1774: 5 — Jayaswirya 12378: 3 — Junghuhn 1079: 20 — Jussieu 17208: 3.
- Kajewski 400: 12; 1308: 4; 1619: 10 — Kanehira 233: 12; 1189: 12; 2408: 12; 3743: 12; 3950: 11 — Kaslind 14783: 3 — Keith 11355: 14; 12768: 14; 16087: 14; 16569: 14 — Kerr 999: 26; 3206: 33; 5347: 33; 5645: 33; 5737: 37; 5944: 26; 8858: 16; 10208: 37; 10868: 21; 10972: 21; 14058: 36; 16079: 36; 16198: 37; 19763: 37; 19963: 37; 20299: 37 — King 4871: 21 — Kingdon Ward, see Ward — Klemme 15219: 14 — Kondo 32862: 14 — Kondo & Edaño 36768: 13; 38877: 14 — Koorders 961: 20; 1563: 20; 1564: 20; 12727: 20; 16648: 14; 20106: 20; 24998: 20 — Korthals 961: 20 — Kurz 2322: 16; 2622: 16.

- LAE series 52094: 10; 52546: 11; 53828: 10; 59094 (Foreman & Stocker): 5; 60256 (Foreman & Vinas): 11; 60454 (Foreman & Stocker): 5; 60493 (Foreman & Stocker): 5; 61174 (Croft et al.): 11; 68785A (Croft et al.): 11; 70805 (Katik): 15; 76964 (Gideon): 19 — Lakshnakara 999: 37 — Lam & Meeuse 6182: 3 — Larsen 8102: 37; 30984: 21 — Larsen et al. 1263: 21 — Lauterbach 475: 11; 1345: 11 — Lazarides 6624: 28; 7650: 9 — Leschenault 814: 1 — Loher 4153: 22; 4844: 22; 7133: 22 — Lörzing 12206: 14; 16881: 14 — Lullfitz 57: 9 — Lütjeharms 4691: 14.
- Mackee 4038: 12; 7884: 12; 8375: 5; 9610: 4; 10048: 12 — Maconochie 608: 6; 724: 28; 725: 28; 962: 6; 967: 28; 968: 28; 1127: 29; 1196: 8; 1238: 7; 1242: 7; 1264/5: 7; 1269: 8; 1272/3: 8; 1283: 8; 1285/6: 8; 1303: 28; 1314: 28; 1315: 28; 1316: 7; 1317: 28; 1318: 28; 1319: 7; 1320-23: 7; 1464-66: 6; 1471: 6; 1477/8: 6; 1508: 6; 1511: 6; 1514: 6; 1516: 6; 1556: 6; 1620: 6; 1622: 6; 1658: 6; 1661: 6; 1722: 4; 1724: 6; 2068: 28; 2069: 28; 2133-35: 6; 2495: 6; 2498: 6; 2667: 6; 2669: 6; 2692: 8; 2694: 8; 2718: 4; 2725: 4; 2726: 4; 2735: 6; 2756: 6; 2762: 4 — Madulid et al. 7232: 22 — Marcan 891: 37 — Mark 714: 1 — Martin 1374: 37 — Matiwang 253: 14 — Maxwell 75-215: 37; 75-237: 37; 76-264: 37; 76-272: 37 — McClure 13315: 18 — McDonald 1534: 4 — McGregor 42080: 22 — McKean 1336: 6 — McPaul 13198: 12 — Meebold 8166: 16 — Melville et al. 3673: 4 — Merrill 657: 25; 855: 13; 3257: 13; 9795: 22; 11386: 14; 18752: 17; 24? — Metz 169a: 1 — Meyer 2577: 13 — Mondri 136: 14 — Mooney 2867: 2 — Moran 4375: 12 — Morse 273: 31 — Mosely 88: 10 — Murata et al. 49760: 37; 49779: 37 — Murthy 9576: 13 — Must 1076: 28; 1088: 6.
- Neker R-87: 12; 95: 12 — Nelson 1099: 6 — NGF series 1626 (White et al.): 15; 15538: 10; 19739 (Sayer): 10; 24825 (Womersley): 10; 25380 (Gillison): 10; 27783 (Streimann): 15; 28556 (Streimann): 19; 34119: 19; 36761 (Ridsdale & Katik): 11; 38078 (Ridsdale & Katik): 10; 39487 (Streimann): 15; 42149 (Vandenberg): 15; 42232 (Vandenberg & Mann): 10; 46475 (Womersley): 11; 49272 (Henty & Lelean): 15; 49273 (Henty & Lelean): 15; 70598 (Larivita & Mann): 11 — Nicholson 1688: 33; 3078: 16 — Noerkas 481: 13 — Nootboom 5269: 12.
- Ogata 10293: 36 — Ohwi & Okamoto 994: 23.
- Parham 137: 12 — Parks 16336: 12; 16373: 12 — Parry 100: 16 — Perrier de la Bâthie 11784: 3; 15980: 3; 18801: 3 — Pierre 532: 37; 1722: 36; 5516: 36; 5517: 33 — Pleyte 978: 12 — Poilane 2746: 36; 4656: 36; 9095: 36; 9328: 36 — Powell 412: 10 — Prawiroatmodjo & Soewoko 1757: 22 — Pullen 956: 15 — Put 2187: 37.
- Quisumbing 12163: 25; 15845: 25.
- Raap 7: 14 — Ramamoorthy & Gandhi 2687: 1 — Ramos 3281: 13; 22391: 22; 80613: 14 — Ramos & Edaño 48953: 13; 48310: 14; 48912: 22 — Read 2186: 1; 2187: 1 — Ridley 7143: 14 — Rinehart 16143: 12 — Robinson 563: 10; 1304: 36 — Rock 2500: 33; 2654: 18; 2680: 26 — Rodin 503: 12; 563: 12 — van Royen 3300: 10; 4269: 19; 4769: 19; 4790: 11; 5297: 11.
- S series 38561 (Chai et al.): 13; 41866 (Lee): 13 — Saldanha 1519: 1 — SAN series 29392 (Chai): 13; 86704 (Steven & Justina): 14; 86714 (Stone & Anderson): 14 — Sands 1864: 15; 3025: 10 — Sangkachand & Smitinand 234: 21 — Saulière 877: 1 — Saunders 583: 15 — Savatier 1207: 23 — Schiefenhövel 142: 11 — Schmid 857: 37; 872: 31 — Schodde 2582: 15 — Scortechini 913: 36 — Seemann 575: 12 — Seidenfaden 11636: 37; 51483: 37 — Shimizu T22450: 37 — Sinclair 8554: 21 — Sinclair & Kiah SF 40769: 21 — SMHI series 2119 (Podzorski): 13 — Smith 4486: 12 — Smitinand 12242: 14 — Smitinand & Abbe 6349: 33 — Sorenso et al. 864: 37; 1320: 33; 6463: 37 — Specht 1003: 6 — Stadman 12: 3 — Stainton 5733: 16; 6638: 16 — van Steenis 3162: 20; 17625: 37 — Steere 11: 23; 16: 12; 17: 12; 19: 12 — Stone 4110: 12 — Swinhoe 4119: 17.
- Takamatsu 1849: 12 — Tanaka 10451: 24 — Thompson 406: 12 — Thorel 374: 36; 2189: 37 — Thwaites 423: 2; 3862: 3; 3689: 2 — Togashi et al. 10074: 23 — Tsou et al. 424: 24.
- UPNG series (Frodin) 4031: 11.
- Versteeg 1470: 11 — Viguier & Humbert 2000: 3 — de Vogel 3136: 23; 5304: 22; 5734: 22 — de Vriese 11153: 20; 11154: 20.
- Wallich 8587B: 1; 8587C: 21; 8587D: 16 — Wang 2737: 18; 75868: 33; 78922: 33 — Wang & Liu 2741: 18; 2743: 18 — Wang & Peng 2673: 18; 2675: 26; 2964: 33; 2977: 18 — Warburg 21129: 11 — Ward 21772: 16; 37538 (SFN): 36 — Waterhouse 356B: 12 — Watt 6796: 16 — Weber 3:

- 14 — White 3406: 4; 10190: 4 — Whitford 1235: 13 — Whiting C25: 12 — Williams 148: 3; 2890: 14; 3058: 14 — Wilson 8058: 23; 10888: 7 — Winit 1686: 33 — Womersley & Hoogland 5158: 15 — Womersley & van Royen 5872: 19 — Womersley & Simmonds 5091: 15 — Wright 2756: 1.
- Yang 557: 38; 563: 38; 729: 38; 733: 38 — Yang et al. 649: 36; 650: 36; 713: 34 — Yuncker 15485: 12.
- Zollinger 1161: 20.

INDEX TO NAMES

Numbers refer to the numbers of the species under which each name can be found; accepted names are in Roman type, the new names and combinations are in **bold** type, and synonyms are in *italics*. For *Epicycas* the numbers are prefixed by 'E'.

Cycas L. [p. 354]

subg. *Cycas* [p. 357]

subg. **Pectinata** de Laub. [p. 375]

subg. **Revoluta** de Laub. [p. 382]

subg. **Truncata** de Laub. [p. 367]

sect. *Asiorientales* J. Schust. = subg. *Revoluta*

sect. *Indosinenses* J. Schust. = *Epicycas*

sect. *Lemuricae* J. Schust. = subg. *Cycas*

sect. *Stangerioides* Smitinand = *Epicycas*

angulata R. Br. 6

apoa K.D. Hill 11

arenicola K.D. Hill 9

armstrongii Miq. 5

arnhemica K.D. Hill 6

badensis K.D. Hill 6

baguanheensi Cheng & Cheng 26

balansae Warb. 63

basaltica C.A. Gardner 8

beddomei Dyer 27

bellefontii L. Linden & Rodigas E3

bougainvilleana K.D. Hill 10

brunnea K.D. Hill 6

cairnsiana F. Muell. 30

calpicola Maconochie 28

campestris K.D. Hill 19

canalis K.D. Hill 7

var. *carinata* K.D. Hill 6

celebica Miq. 12

chamberlainii W.H. Br. & Kienholz 22

chevallieri Leandri E3

circinalis L. 1

var. *angustifolia* Miq. 1

var. *beddomei* (Dyer) J. Schust. 27

var. *currantii* J. Schust. 13

var. *javana* Miq. 20

var. *orixensis* Haines 2

var. *pectinata* (Griff.) J. Schust. 16

var. *scratchleyana* (F. Muell.) J. Schust. 11

(Cycas circinalis)

subsp. *madagascariensis* (Miq.)

J. Schust. 3

subsp. *papuana* (F. Muell.) J. Schust. 5

subsp. *riuminiana* (Porte ex Regel)

J. Schust. 22

subsp. *seemannii* (A. Braun) J. Schust. 12

subsp. *thoursii* (Desf. ex Gaudich.)

J. Schust. 3

comorensis Bruant 3

conferta Chirgwin & Wigston 7

couttsiana K.D. Hill 6

desolata P.I. Forster 6

dilatata Griff. 16

edentata de Laub. 14

ferruginea Wei 18

furfuracea W. Fitzg. 9

glauca Lam. ex Loudon 10

glauca Miq. 10

gracilis Miq. 4

guizhouensis Lan & Zhou 18

hainanensis Chan et al. 17

immersa Craib 26

inermis Lour. 23

javana (Miq.) de Laub. 20

jenkinsiana Griff. 16

kennedyana F. Muell. ex Warb. 4

lanepoolei Gardner 7

lindstromii S.L. Yang & K.D. Hill E8

longipetiolula D.Y. Wang E2

longlinensis Chang & Y.C. Zhong 18

maconochiei K.D. Hill 6

macrocarpa Griff. 21

madagascariensis Miq. 3

media R. Br. 4

var. *basaltica* (C.A. Gardner) J. Schust. 8

var. *furfuracea* (W. Fitzg.) J. Schust. 9

var. *lanepoolei* (C.A. Gardner) J. Schust. 7

(Cycas)

- megacarpa* K.D. Hill 4
micholitzii Dyer E1
 var. *simplicipinna* Smitinand E3
micronesica K.D. Hill 12
miquelii Warb. E5
multifida Chang & Y.C. Zhong ?16
multipinnata Chen & Yang E2
nathorstii J. Schust. 2
neocaledonica L. Linden 12
normanbyana F. Muell. 8
ophioliitica K.D. Hill 6
orientis K.D. Hill 6
panzihuanensis Shou & Yang 26
papuana F. Muell. 5
pectinata Buch.-Ham. 16
pectinata Griff. 16
 var. *elongata* Leandri E6
platyphylla K.D. Hill 6
pruinosa Maconochie 29
revoluta Thunb. 23
 var. *inermis* (Lour.) Miq. E4
 var. *taiwaniana* (Carruth.) J. Schust. 24
riuminiana Porte ex Regel 22
rumphii Miq. 10
 var. *bifida* Dyer E1
 var. *seemannii* (A. Braun) Parham 12
 var. *timorensis* Miq. 14
 subsp. *normanbyana* (F. Muell.)
 J. Schust. 8
 subsp. *zeylanica* J. Schust. 3
schumanniana Lauterb. 15
scratchleyana F. Muell. 11
seemannii A. Braun 12
senota K.D. Hill 6

(Cycas)

- shiwandashanica* Chang & Y.C. Zhong E3
siamensis Miq. E7
 subsp. *balansae* (Warb.) J. Schust. E3
 subsp. *inermis* (Lour.) J. Schust. E4
silvestris K.D. Hill 13
sphaerica Roxb. 2
squamosa Lodd. ex Dyer 1
squarrosa Lodd. ex Loudon 1
szechuanensis Chen & Fu 18
taitungensis Shen et al. 24
taiwaniana Carruth. 17
thouarsii Desf. ex Gaudich. 3
tonkinensis (L. Linden & Rodigas) L. Linden
 & Rodigas E3
tuckeri K.D. Hill 6
undulata Desf. ex Gaudich. 1
wadei Merr. 25
wallichii Miq. 1
xilingensis Chang & Y.C. Zhong 18
xipholepis K.D. Hill 7
yorkiana K.D. Hill 6
Epicycas de Laub. [p. 388]
elongata (Leandri) Yang E6
lindstromii (Yang & K.D. Hill) de Laub. E8
micholitzii (Dyer) de Laub. E1
miquelii (Warb.) de Laub. E5
multipinnata (Chen & Yang) de Laub. E2
siamensis (Miq.) de Laub. E7
spec. nov. 1 E4
tonkinensis (L. Linden & Rodigas)
 de Laub. E3
Zamia L.
corsoniana G. Don 10
tonkinensis L. Linden & Rodigas E3

A TAXONOMIC REVISION OF PLAGIOGYRIACEAE (PTERIDOPHYTA)

XIAN-CHUN ZHANG¹ & H.P. NOOTEBOOM²

SUMMARY

A taxonomic revision of Plagiogyriaceae is presented. One genus and 11 species are recognised. One species, *P. egenolfoides*, is subdivided into four varieties. Only one species, *P. pectinata*, occurs in the New World, all others in the Old World. One species, *P. glauca*, and one variety, *P. egenolfoides* var. *decrescens*, extend east to the S Pacific islands (Solomons).

INTRODUCTION

As a preliminary result of the current study, eleven species are recognised. Most of the wide-spread species are represented by local populations with diverse ranges of variation. This resulted in the past in endless unnecessary splitting based on a number of mostly overlapping characters, like the form of the frond-apex (pinna-like or not), the degree of pinna margin serration, aerophores' appearance, and the size of specimens. The number of species accepted here agrees with that in Christensen's index (1906), and also with the estimates of Tryon & Tryon (1982), and Tryon & Stolze (1989). Tryon also correctly predicted that there is not such a large diversification in *Plagiogyria* as recognised by some botanists.

Under 'Morphology' the paragraphs about the spores is written by Dr. G.A. van Uffelen.

MATERIAL AND METHODS

During our joint research on Plagiogyriaceae for a revision for Flora Malesiana, most of the important types housed in American, European, Japanese, and Indonesian herbaria were available on loan or in the herbaria visited. Those of Blume, Rosenstock, Alderwerelt and Raciborski are in Leiden and those of Ching in Beijing. A total of about 1700 collections represented by more than 3000 herbarium sheets were studied with the aid of computer programmes for handling taxonomic collections and literature. These programmes were devised by the second author using Dbase IV. Further DELTA, TAXASOFT, and KCONI were used for technical and key descriptions.

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