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An Essay on Metroxylon, the Sago Palm

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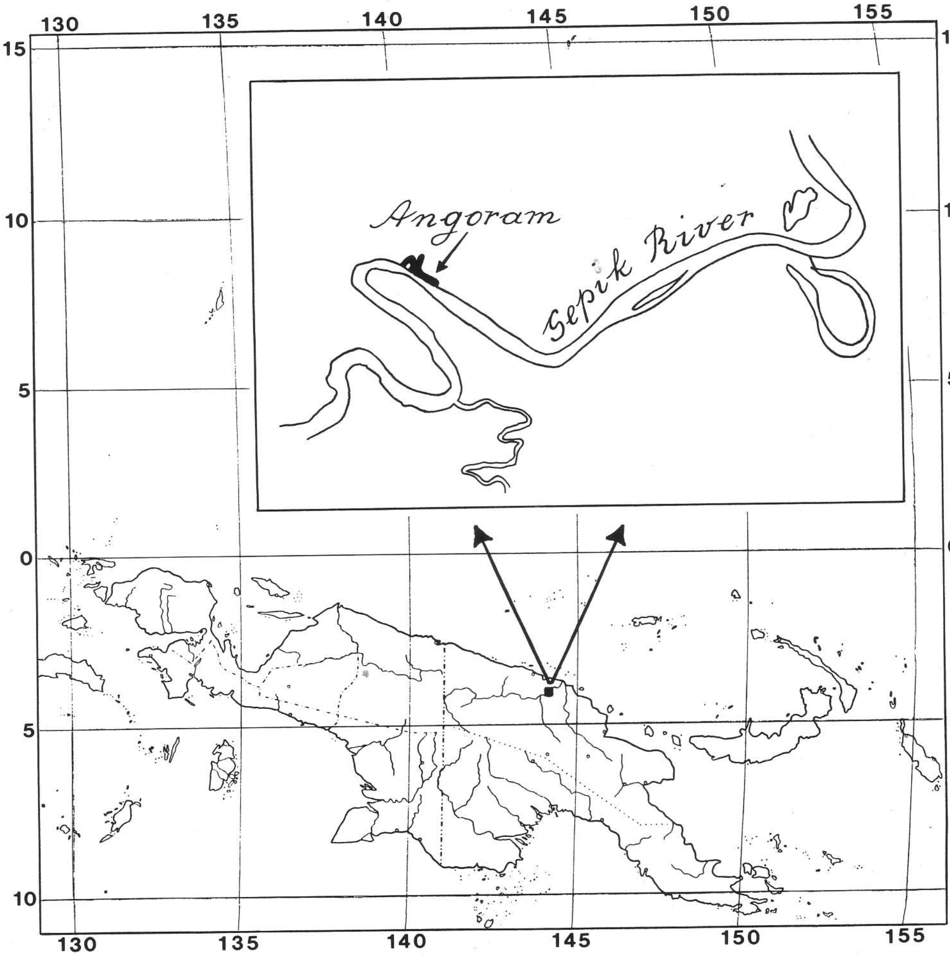
Metroxylon is a genus of arborescent palms of Papuasia and several island groups of Micronesia and Melanesia. There are five species occurring in five separate areas. The most widespread taxon, *M. sagu,* covers Malaysia, Indonesia, Mindanao, and New Guinea. The other four taxa are endemic to the aforementioned island groups.

The palms accumulate starch in the pith of their trunks and are a traditional source of carbohydrate. The best known representative of the genus in this respect is *M. sagu,* known as the sago palm. This species occupies the largest area, estimated to cover 4 million ha in natural stands and about .2 million ha under cultivation. With the exception of *M. salomonense,* the other species of *Metroxylon* are not exploited for their starch content. At present, interest on *Metroxylon* as a starch-producing crop is focused on *M. sagu* which grows in swampy areas usually unsuitable for plantations of other crops. So far, two international symposia have been held to evaluate the exploitation of sago starch (Sago 1977, Sago 1980). In addition, an FAO expert consultation took place in Jakarta in 1984. Studies were carried out in Indonesia (Team Proyek 1982) and Papua New Guinea (DME 1980, 1982).

The present author has made a taxonomic survey for the Papua New Guinean government in the Sepik River flood plain (Fig. 1). An estimated one million ha of natural sago palm stands occur in PNG, and an additional 20 thousand ha are under cultivation. The aim of my survey and the present paper has been to report on the variability of *M. sagu* in PNG, in the context of the diversity found in the genus as a whole. This paper may contribute towards an eventual monograph of *Metroxylon.*

History of the Genus

The first and most competent publication on sago palms is by Rumphius (1741). In the *Herbarium Amboinense* he gives a meticulous description of the sago palm as it occurs in Ambon, and he presents the taxonomic views of the inhabitants on this palm. Four Ambonese species are described under the generic name of *Sagus.* This name was adopted by Gaertner (1788), but unfortunately also included *Raphia* P. de Beauvois. Giseke (1792) does not include *Raphia* and gives the earliest binomial applying solely to the description of Rumphius's *S. genuina.* The name *Sagus* is, however, antedated by *Metroxylon* Rottboell (1783), based partly on Rumphius's description, but in larger part on specimens provided for Rottboell by Dr. Koenig. The next author to adopt *Metroxylon* was Von Martius (1845). Nearly eighty years after Rottboell, Wendland (1862) proposed the generic name *Coelococcus* in which he described a sago palm from the Fiji Islands. *Coelococcus* has henceforward been adopted by various other authors (Dingler 1887, Warburg 1896, Heim 1904) to classify several species of sago palm from



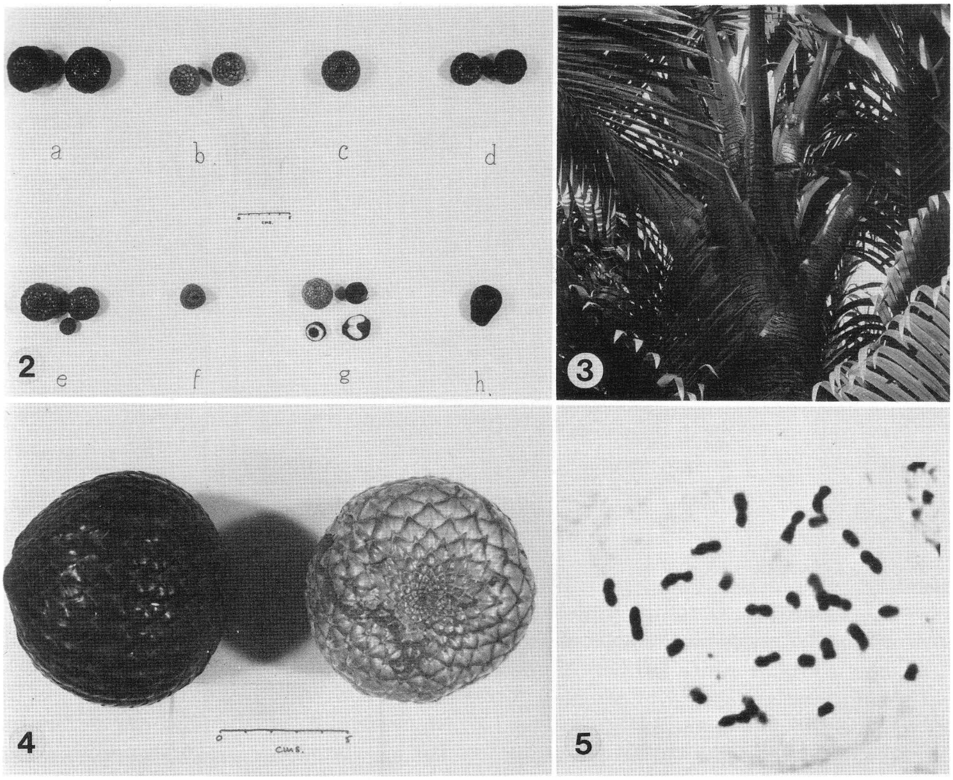
1. Papua New Guinea with an enlarged inset showing where the author made his collections.

Micronesian and Melanesian islands; *Metroxylon* is used exclusively for those sago palms occurring throughout New Guinea, Indonesia, and Malaysia. Beccari (1918) included *Coelococcus* in *Metroxylon* as a section, an opinion that has since been followed. Some commotion may have arisen in the early sixties when Moore (1962) disclosed that Rottboell's *Metroxylon* is actually antedated by *Sagus* Steck (1757). However, Steck's publication is not effectively published, and *Metroxylon* Rottb. is conserved (1968) against this name.

Diagnostic Characters

A brief treatment of the diagnostic characters within *Metroxylon* is appropriate. Especially where the inflorescence is concerned, the application of correct terminology to refer to particular units is vital. In this paragraph, diagnostic characters are treated in an order reflecting the comparative importance of each character within the taxonomy of the genus: the most significant character is treated first.

Inflorescence: The inflorescence of



2–5. 2. Fruits of *Metroxylon sagu*. 3. Spines on leaf sheaths and petioles of a mature specimen. 4. Fruits of *M. amicarum*. 5. *M. sagu*, somatic chromosomes in equatorial plane (photo by J. C. Arends).

Metroxylon is extensively discussed in Tomlinson (1971). For reasons of brevity of this paper, reference to this publication is made for interested readers. As far as diagnostic characters are concerned, the shape of specific units of the inflorescence has proved useful. Most characteristic is whether branches of a certain order are pendulous or not. This single character enables unambiguous distinction of three out of the five species recognized in *Metroxylon*.

Fruits (Figs. 2,4): The fruits of *Metroxylon* are covered with longitudinal series of imbricate rhomboidal scales (Fig. 4). The apex of the fruit is always mucronate, the mucro representing the remains of the style. Although the pistil of *Metroxylon* is three-locular with a single basal ovule in each locule, usually only a single seed matures in each fruit. This seed contains a considerable amount of hard, bony, homogenous endosperm which has a very characteristic horseshoe shape in vertical section, with a large chalazal cavity. The embryo is situated in a smaller, second peripheral cavity. Differences between the taxa are found in the number of longitudinal series of scales on the fruit. The division of the genus into two sections is based upon the number of scales. At the specific level, the shape and the size of the mature fruit is also diagnostic.

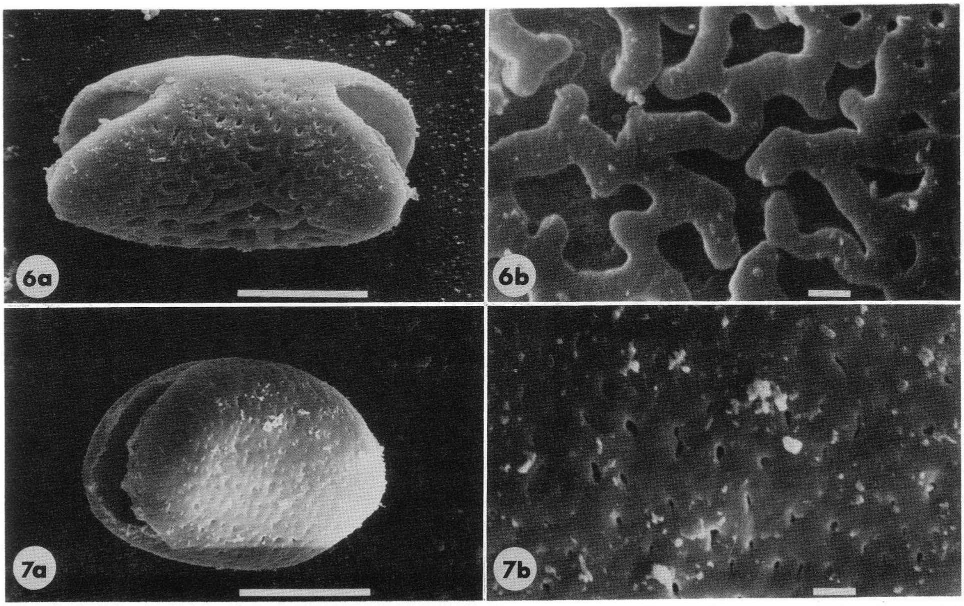
Spines (Fig. 3): Spinescence has been emphasized in *Metroxylon* as an important diagnostic character throughout. Authors, such as Rumphius (1741) and Beccari (1918), as well as sago-subsisting people, all greatly value spinescence in their respective taxonomies. Among other things this led to the division of the section *Metroxylon* into 17 taxa by Beccari. However, in the section *Coelococcus* he distinguished 7 taxa only. Probably this was because Beccari lacked the extensive collections and experience in the field with these taxa that he had in *Metroxylon*. Like Beccari, the present author is familiar with the section *Metroxylon*, but has scant knowledge of *Coelococcus* apart from herbarium specimens and descriptions. According to the data, all taxa in the section *Coelococcus* are spinescent, but details such as length and abundance of spines are not available. Such characters enable me to distinguish between taxa in the section *Metroxylon*, and they may be of the same value in the section *Coelococcus*. Spines are found in transverse crescent-shaped series on the abaxial side of a leaf, over the entire surface of the leaf sheath, and along a strip of about 3 cm wide on the petiole and rachis. Spines are pectinate, flattened, of a brownish color, and confluent by their bases, i.e. arranged as in a comb (Figs. 12,13). Their length ranges from a few cm up to 22 cm. Furthermore, they are unequal, the middle one of a series usually being the longest. Reduction in length of spines occurs, in which case they are referred to as spinules. Spinules are short, up to 10 mm long, and usually of a triangular form. The ultimate reductions of spines are knoblike structures which occur exclusively on the base of leaf sheaths. The variability in spine morphology in the section *Metroxylon* is threefold. The first is related to the age of the palm. Crown leaves of a mature specimen usually have spines that are much shorter than those on leaves from offshoots of the same palm. Secondly, the exact location of the spines is important. Especially in a mature palm, the spines on the leaf sheath are longer than the spines on the petiole and rachis. In the third place, I am of the opinion that the length of spines may be governed by a comparatively simple genetic mechanism. Thus, different *formae* in the section *Metroxylon* (e.g. spiny vs. smooth) are considered to be only slightly different genotypes of a single species, *M. sagu*, instead of two or more different species or subspecies. This assumption will be dealt with in the Discussion.

Somatic Chromosome Numbers: Somatic chromosome numbers of *M. sagu* were determined from root tips of

1) Seedlings grown at the Department of Plant Taxonomy at Wageningen. The seeds were collected in the Sepik area (PNG) by Mr. Van Kraalingen and all specimens were spiny. One seedling has been preserved at WAG (*Rauwerdink 138*).
2) Plants grown at the Department of Tropical Crop Science at Wageningen, from seeds obtained from the Singapore Botanical Gardens. Spiny as well as unarmed plants were available.

Permanent squash preparations were made according to the methods described in De Wilde and Arends (1979). The slides are retained in the slide collection of the Department of Plant Taxonomy. No living material from the other taxa in *Metroxylon* was available for an investigation. The Singapore plants had already been investigated by Verhaar (1977) at $2n = 26$. The present author also obtained the somatic chromosome number of $2n = 26$ in *M. sagu* (Fig. 5), both in the PNG specimens and in the Singapore material. The basic chromosome number of *M. sagu* can therefore be put at $x = 13$, which actually marks *M. sagu* as an exception in Calamoid palms. The basic chromosome number in these palms is $x = 14$, according to Moore and Uhl (1982).

Analysis of Pollen: Recent analyses on the pollen morphology of *Metroxylon* were undertaken by Sowumni (1972) and Thanikaimoni (1970). This paragraph presents a few observations by the latter



6–7. 6. Scanning electron microscope (SEM) photo of a pollen grain; a, *Metroxylon sagu*, overview, bar = 1.0 micrometers; b, detail of exine sculpture, bar = 0.1 micrometers. 7. SEM photo of a pollen grain of *M. warburgii*; a and b, as above for *M. sagu*.

author on the sculpture of the exine in *Metroxylon*.

Pollen grains were obtained from herbarium specimens on loan from various institutions. The specimens analyzed are listed below. Voucher slides of pollen have been filed at Wageningen and the respective institutions.

M. sagu: Bakhuizen v/d Brink 7488 (B).
M. salomonense: Moore 9317 (K).
M. vitiense: Smith 9339 (K).
M. amicarum: leg. *Kramer* s.n. (B) and *Furtado 25868* (K).
M. warburgii: Moore 9319 (P).

Pollen grains have been analyzed with the scanning electron microscope (SEM) and with the light microscope (LM). Samples were prepared according to the acetolysis procedure that is commonly used at the Department. The pollen grains of all taxa in *Metroxylon* are dicolpate, i.e. possessing two germination apertures. They are oval, about 30 μm long and about 15 μm wide. On the basis of the sculpture of the exine of the grains, the genus can be divided into two groups. One group has a reticulate ornamentation on the equatorial sides. The lumina of this reticulum diminish in size towards the colpi, resulting in a perforate tectum (Fig. 6a,b). This group consists of *M. salomonense* and *M. vitiense*. The other group displays a perforate tectum over almost the total surface of the grain (Fig. 7a,b). This group consists of *M. warburgii*, *M. amicarum*, and *M. sagu*. The exine-sculptural types I found were also recognized by Thanikaimoni and Sowumni; neither author, however, had the opportunity to investigate all taxa in the genus. Thanikaimoni used the terms coarsely reticulate and finely reticulate for the exine sculpture of *M. salomonense* and *M. sagu* respectively. Sowumni uses the terms reticulate and vermiculite. Praglowski and Punt, in their 1973 paper, propose the definitions for exine sculpture which I have adopted here. At present, it is difficult to relate the two types of pollen grains in *Metroxylon* to the taxonomy of the genus. The division of *Metroxylon* into two sections based on fruit characters is not paralleled by a division based on pollen types.

Taxonomic Treatment

Metroxylon Rottboell in Nye S. Kon. D. Vid. Sels. Skr. 2: 527. 1783 nom. cons.: Koenig in Ann. of Bot. ed. K. & S. 1: 193. 1804; Endlicher in Gen. Pl. Sec. Ord. Nat.: 250. 1837; Kunth in Enum. Pl. 3: 213–215. 1841; Meisner in Pl. Vasc. Gen. 1: 354(265). 1843; Martius in Hist. Nat. Palm. 3: 213. 1845 (ex parte *Pigafetta* Blume); Miquel in Fl. Ind. Bat. 3: 139. 1855 (ex parte *Pigafetta* Mart.); Drude in E. & P. Pfl. Fam. 2(3): 47. 1887; Beccari in Ann. Royal Bot. Gard. Calc. 12, 2: 156–157. 1918; Ridley in Fl. Mal. Pen. 5: 31. 1925; Blatter in Palms Brit. Ind. & Ceylon: 256–259. 1926; Lawrence in Gent. Herb. 8: 438. 1956. Type: *M. sagu* Rottboell.

Sagus Steck in De Sagu 21. Diss. Inaug. Medica de Sagu. 1757. Nominum invalidum teste Moore in Taxon 11: 164–166. 1962 and Taxon 17: 85. 1968.

Sagus Giseke in Prael. Ord. Nat. Pl.: 93. 1792 (excl. *S. palmapinus* et *S. filaris*); Blume in Rumphia 2: 144–154, t. 86, 126 and 127. 1843 (ex parte *Pigafetta*); Griffith in Palms Brit. Ind. 24: 18–20. 1850. Type: *S. genuina* in Herb. Amb. 1: 75. 1741.

Coelococcus H. A. Wendland in Bonplandia 10: 199. 1862. Type: *C. vitiense* H. A. Wendland.

Arborescent, solitary or clustering, armed or unarmed, pleonanthic or hapaxanthic, polygamous palms of lowlands and swamps, also known from hillsides. Trunk columnar, to 20 m, ringed with leaf scars and partly covered with clasping, persistent leaf sheaths. Leaves pinnate, erect, spreading and eventually horizontal; sheath broad, clasping the trunk, having semicircular transverse ridges bearing series of ± conspicuous spines, prickles or knobs, or totally smooth: petioles up to several meters in tillers but considerably shorter in mature leaves, strongly channeled, abaxially convex, sometimes armed with transverse series of ± conspicuous spines or prickles, adaxially concave; rachis straight, if armed, similar to the petiole along its convex abaxial side, the adaxial side bifaced with the salient angle smooth; pinnae straight to drooping, ± equidistant or in clusters, green and shiny, faintly paler underneath, linear, unicostate, acute with a spinulous costa and margins. Inflorescences each branching to five orders, the bracts sometimes covered with spinules, sometimes in transverse series. Flowers reddish-brown, arranged in dyads of one male and one hermaphrodite flower each, similar in appearance, the dyads very regularly distributed along third-order axis in spirals, depending on developmental stage, ± immersed in the reddish-brown (greyish) hairs of the flower bracts. Male flower borne on one side of the hermaphrodite; precocious and dropping before anthesis of the hermaphrodite; calyx ± deeply three-lobed in the upper third, the lobes broadly rounded at the apex, coriaceous, ovate, obtuse, tapering below to a narrow base; the corolla 1½ to more than 2 times longer than the calyx, divided in its upper two-thirds into three ± woody, oblong-ovate, glabrous, boat-shaped segments, the lower part entire, campanulate: stamens 6, the united bases of the filaments forming a cup adnate to the undivided part of the corolla, broadly linear in their free part, flattened: anthers elongate-elliptical, obtuse, cells parallel, latrorse, bases disjunct, dorsally attached to the filaments at the middle of the connective: ovary rudimentary, represented by three, small, ± coalescent, oblong bodies, merging into a prominently three-sided style. Hermaphrodite flower with calyx, corolla and androecium similar to the male flower; ovary globose and shiny with yellowish rhomboidal scales, trilocular, ovules 3, reportedly basal, erect, anatropous; style narrow, prominently three-sided, grooved. Fruits covered with scales, containing one seed.

Key to the Species of Metroxylon

1. Fruit covered with 18 longitudinal series of scales. Clustering palm, unarmed or spiny to various degrees (section *Metroxylon*) New Guinea, Indonesia, Mindanao, Malaysia .... 1. *M. sagu*
1. Fruit covered with (22) 24–28 longitudinal series of scales. Spinescent, solitary palms lacking basal offshoots (section *Coelococcus*) 2
2. Inflorescences seemingly lateral, first-order branches arising from the axils of unreduced crown leaves. Guam, Caroline Islands and planted in the Philippines .... 3. *M. amicarum*
2. Inflorescences seemingly terminal, first-order branches arising from the axils of reduced, bractlike, crown leaves 3
3. Second-order branches of the inflorescence pendulous, very short (20 cm). Fiji Islands .... 3. *M. vitiense*
3. Second-order branches not pendulous 4
4. Third-order branches of the inflorescence pendulous, very long (20 cm), adaxial pedicellar parts of all branches pubescent. Solomon Islands, Bougainville, St. Cruz Island .... 4. *M. salomonense*
4. All branches of the inflorescence erect. Adaxial pedicellar parts of all branches not pubescent. New Hebrides, Western Samoa .... 5. *M. warburgii*

1. **Metroxylon sagu** Rottboell in Nye. S. Kon. D. Vid. Sels. Skr. 2: 527. 1783; Miquel in l.c.: 147. 1855; Beccari in N. Giorn. Bot. Ital. 3: 29. 1879; Hooker in Fl. Brit. Ind. 6: 481. 1894; Beccari in Denk. K. Akad. Wiss. M. Nat. Kl., Wien, 84: f. 6. 1913. Type: Koenig specimens and drawings and Rottboell l.c. 1783.

Sagus sylvestris Rumphius in l.c.: 75. 1741; Blume in l.c.: 153. 1843.

Sagus genuina bis sylvestris Giseke in l.c.: 94. 1792.

Metroxylon sylvestre Martius in l.c.: 215. 1845; Miquel in l.c.: 146. 1855.

Metroxylon rumphii Mart. var. *sylvestre* Beccari in Ann. Royal Bot. Gard. Calc. 12, 2: 174, p. 107. 1918. Type: *Sagus sylvestris* in Herb. Amb. 1: 75. 1741.

Metroxylon rumphii Mart. var. *ceramense* subvar. *ceramense* Beccari in l.c.: 175, p. 107. 1918.

Metroxylon rumphii Mart. var. *ceramense* subvar. *platyphyllum* Beccari in l.c.: 175. 1918. Type: *Beccari 12* (isotype at BO).

Metroxylon rumphii Mart. var. *ceramense* subvar. *rubrum* Beccari in l.c.: 175. 1918. Type: *Beccari 8* (isotype at BO).

Metroxylon rumphii Mart. var. *ceramense* subvar. *album* Beccari in l.c.: 175. 1918. Type: *Beccari* s.n. (isotype at BO).

Sagus genuina (excl. *Sagou duri-rottang*) Rumphius in l.c.: 75. 1741; Blume in l.c.: 150. 1843.

Sagus rumphii Willdenow in Sp. Pl. 6: 404. 1805.

Sagus spinosus Roxburgh in Fl. Ind.: 623 excl. syn. 1832.

Metroxylon rumphii Martius in l.c.: 214. 1845; Miquel in l.c.: 140. 1855; Beccari in N. Giorn. Bot. Ital. 3: 30. 1879 et in Malesia 1: 91. 1887; Hooker in Fl. Br. Ind. 6: 481. 1894. Type: *Sagus genuina* in Herb. Amb. 1: 75, t. 17. 1741.

Metroxylon rumphii Mart. var. *ceramense* subvar. *nigrum* Beccari in Ann. Royal Bot. Gard. Calc. 12, 2: 175. 1918. Type: Beccari s.n. (isotype at BO).

Metroxylon rumphii Mart. var. *buruense* Beccari in l.c.: 177–178. 1918. Type: *Labillardiere* s.n.

Metroxylon squarrosum Becc. var. *squarrosum* Beccari in l.c.: 179–180. 1918.

Metroxylon squarrosum Becc. var. *kilwoi* Beccari in l.c.: 180. 1918. Type: *Beccari 1* (isotype at BO).

Metroxylon squarrosum Becc. var. *killasi* Beccari in l.c.: 180. 1918. Type: *Beccari 2* (isotype at BO).

Metroxylon squarrosum Becc. var. *kilkarua* Beccari in l.c.: 180. 1918. Type: *Beccari 3* (isotype at BO).

Metroxylon squarrosum Becc. var. *kilatan* Beccari in l.c.: 181. 1918. Type: *Beccari* s.n. (probably 4, isotype at BO).

Metroxylon squarrosum Becc. var. *kilkour* Beccari in l.c.: 181. 1918. Type: *Beccari* s.n. (probably 5, isotype at BO).

Metroxylon squarrosum Becc. var. *kiltafuk* Beccari in l.c.: 181. 1918. Type: *Beccari 6* (isotype at BO).

Metroxylon squarrosum Becc. var. *kilkikir* Beccari in l.c.: 181. 1918. Type: *Beccari* s.n. (probably 7, isotype at BO).

Metroxylon rumphii Mart. var. *flyriverense* Beccari in l.c.: 178–179. 1918. Type: *D'Albertis* s.n.

Metroxylon oxybracteatum Warburg ined. nomen nudum; Schumann & Lauterbach in Fl. d. Sudsee: 202. 1901.

Clustering palm, 8–20 m high, stem 15–60 cm diameter near base; leaves up to 7 m in mature palms, up to 12 m in vigorous offshoots, unarmed or ± armed with spines or spinules on transverse ridges or series. Inflorescence apparently terminal with first-, second-, and third-order branches erect to spreading (Fig. 8). Bracts of first, second, and third order with spinules or smooth; in hermaphrodite flower, style attains apex of the anthers at anthesis. In male flower ovary rudimentary and style not exceeding filaments. Fruit globose, apple-shaped to shaped like an inverted pine cone, very variable in shape and size within an inflorescence, 4–4.5 cm broad, 18 (19) longitudinal series of straw colored scales; seed frequently abortive, fruit then filled with a fleshy hypertrophic mass.

Distribution: New Guinea and widely planted throughout Indonesia, Malaysia, and the Philippines.

Vernacular Names: sak-sak, rumbia, kiraj, ambulung, lapia, sagu, lumbia, pohon sagu.

Specimens Examined: These specimens have been identified as belonging to the species *M. sagu*, but a further identification as one of the four formae in *M. sagu* has not been possible (veg. = vegetative, i.e. no flowers or fruits available; fl. = displaying flowers; fr. = displaying fruits; pfl. = the specimen is past flowering but has not formed any fruits). NEW GUINEA. Sepik, 1953, *Floyd 5409* (fl. BO, L); Vogelkop, 1948, *Kostermans G et H* (fr., BO). INDONESIA, CELEBES, 1895, *Koorders 19722* bis (veg., BO, L); SUMATRA, Korthals s.n. (veg., L); JAVA, 1903, *Schoute* s.n. (fl., L), 1882, *Treub* s.n. (fr., B), 1885, *Treub* s.n. (fr., B); BATJAN, 1883, *Warburg* s.n. (fr., B); CULTA, 1909. *d'Alleizette 7715* (fr., L, SBG). 1922. *Bakhuizen v/d Brink 1544* (fr., BO), 1958, *Heine s.n.* (fr., BO), 1899, *Koorders 35664* bis (fr., BO), *Schlechter* s.n. (fr., B).

Key to the Formae of M. sagu

1. Leaf sheaths and petioles at all ages of the palm unarmed, totally smooth .... forma *sagu*
1. Leaf sheaths and petioles not quite smooth or armed 2
2. The bases of leaf sheaths at all ages of the palm with knob-like structures (spine reductions) .... forma *tuberatum*
2. The leaf sheaths and petioles bearing spines ... 3
3. Leaf sheaths and petioles bearing spines shorter than 4 cm .... forma *micracanthum*
3. Leaf sheaths and petioles bearing spines of 4–20 cm long .... forma *longispinum*

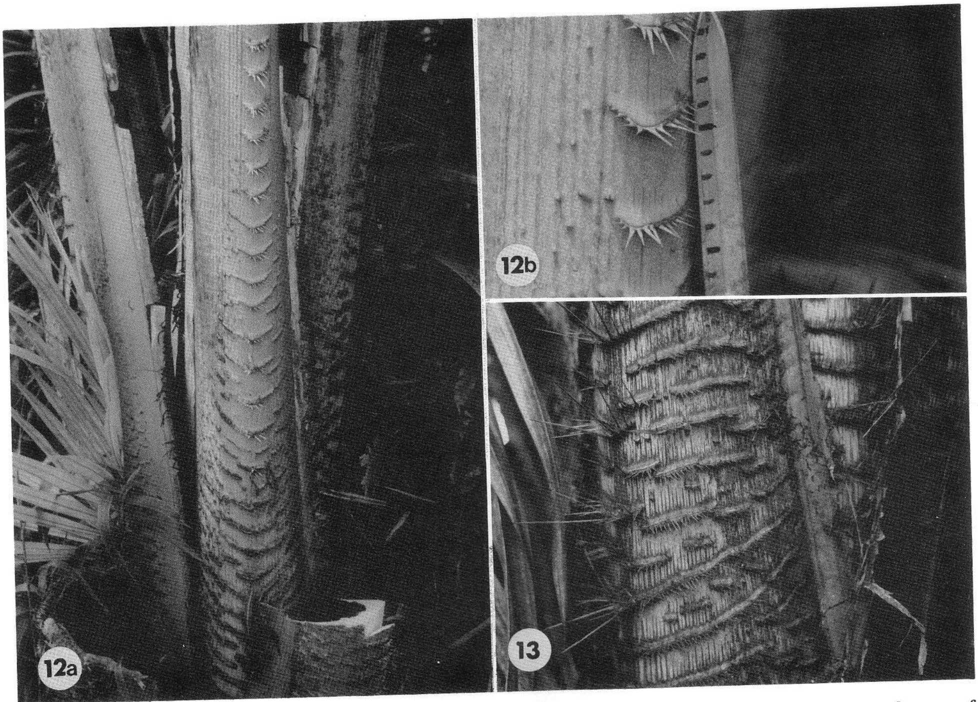
1a. **Metroxylon sagu** forma **sagu** (Fig. 9).

Sagus laevis Blume in l.c.: 146. 1843.

Metroxylon laeve Martius in l.c.: 214. 1845. Typus: Koenig specimens ad Rottboell et Rottboell ut omittam quo ad Rumphius.

Sagus laevis Rumphius in l.c.: 76. 1741; Griffith in Calc. J. Nat. H. 5. 1845 et in Palms Br. Ind. 24. 1850.

8–11. 8. *Metroxylon sagu*, habit showing "terminal" inflorescence. 9. *M. sagu*, forma *sagu*. 10. *M. sagu* forma *tuberatum*. 11. Same, petiole at higher magnification showing knoblike structures (reduced spines).



12–13. 12. *Metroxylon sagu* forma *micracanthum*; a, sheath and base of petiole showing curved rows of spines; b, close up of spines. 13. *M. sagu* forma *longispina*, leaf sheath showing long rows of spines.

Sagus genuina S. laevis Giseke in l.c.: 94. 1792.

Sagus inermis Roxburgh in Fl. Ind. 3: 623. 1832.

Sagus laevis Jack in Comp. Bot. Mag. 1: 266. 1836.

Metroxylon hermaphroditum Hasskarl in Tijd. Nat. Gesch. 9: 175. 1842.

Metroxylon inerme Martius in l.c.: 215. 1845. Typus: *Sagus laevis* in Herb. Amb. I: 76. t. 17. 1741.

Metroxylon sagus Rottb. var. *molat* Beccari in l.c.: 167, p. 107. 1918. Typus: *Beccari 10* (isotype BO).

Metroxylon sagus Rottb. var. *peekelianum* Beccari in l.c.: 167–168. p. 106. 1918. Typus: *Peekel 115* (not seen).

Metroxylon sagus Rottb. var. *gogolense* Beccari in l.c.: 168, p. 106. 1918. Typus: *Lauterbach 861* (not seen).

The leaf sheath, petiole, and rachis of a leaf are entirely devoid of spines, smooth to the touch at all ages of the palm. All bracts of the inflorescence are smooth too. The pinnae may be spinulous at the apex and the costa.

Vernacular Names: ambutrum, kaparang, awirkoma (PNG).

Specimens Examined: NEW GUINEA, Milne Bay, 1953, *Brass 22064* (fr., A, L); Sepik, 1981, *Rauwerdink 112* (fr., WAG), *Rauwerdink 119* (pfl., WAG), *Rauwerdink 123* (veg., WAG), *Rauwerdink 128* (veg., WAG). INDONESIA. SUMATRA, 1933, *Rahmat si Torus 5225* (pfl., A, L). PHILIPPINES. MINDANAO, 1912, *Fenix 1112* (fr., P). 1915, *Miras Medina 24526* (pfl., A). MALAYSIA. SABAH, 1964, *Moore 9218* (fr., BH). CULTA. 1929, *Bakhuizen v/d Brink 7488* (fl., B, BO, L, P), 1952, *Moore 6096* (veg., BH), 1894, *Ridley 6274* (fl., SBG), 1896, *Ridley* s.n. (fr., K).

1b. **Metroxylon sagu** forma **tuberatum** Rauwerdink **form. nov.** (Figs. 10,11) vaginae frondinum tuberatae. Typus: New Guinea. E-Sepik prov., 1981, *Rauwerdink 115* (pfl., holotype WAG; isotypi BO, BH, CANB, K, L, LAE, SIN).

The base of the leaf sheaths covered with knoblike structures, irregular to the touch, at all ages of the palm. Petiole, rachis, and all bracts of the inflorescence perfectly smooth. The pinnae can be spinulous at the apex and costa.

Vernacular Names: koma, oliatagoe (PNG).

Specimens Examined: NEW GUINEA. Sepik, 1981, *Rauwerdink 115* (pfl., WAG), *Rauwerdink 135* (veg., WAG).

1c. **Metroxylon sagu** forma **micracanthum** (Blume) Rauwerdink **stat. nov.** (Fig. 12a,b). Typus: Blume in Rumphia 2: 153 teste Rumphius p. 75, sub. no. 1, Sagu Duri-Rottang.

Sagus duri rottang Rumphius in l.c.: 75. 1741.

Sagus micracantha Blume in l.c.: 153. 1843.

Metroxylon micracanthum Martius in l.c.: 146. 1845; Miquel in l.c.: 146. 1855.

Metroxylon rumphii Mart. var. *micracanthum* Becc. subvar. *micracanthum* Beccari in l.c.: 176. 1918. Typus: *Sagu Duri-Rottang* in Herb. Amb. 1: 75. 1741.

Metroxylon rumphii Mart. var. *micrancanthum* Becc. subvar. *makanaro* Beccari in l.c.: 177. 1918. Typus: *Beccari 14* (isotype BO).

The leaf sheath, petiole and rachis from an early age of the palm with spines not longer than 4 cm. Bracts of the inflorescence smooth or with scattered spinules.

Vernacular Names: makapn, waipi, kangrum, mandm (PNG).

Specimens Examined: NEW GUINEA. Sepik, 1981, *Rauwerdink 114* (fr., WAG), *Rauwerdink 118* (pfl., WAG), *Rauwerdink 127* (fl., WAG), *Rauwerdink 134* (veg., WAG).

1d. **Metroxylon sagu** forma **longispinum** (Giseke) Rauwerdink **stat. nov.** (Fig. 13). Typus: Rottboell pro parte quo ad Rumphius.

Sagus longispina Rumphius in l.c.: 75. 1741; Blume in l.c.: 154. 1843.

Sagus genuina longispina Giseke in l.c.: 94. 1792.

Sagus longissimus Hamilton in Mem. Wern. Soc. 5: 320. 1824.

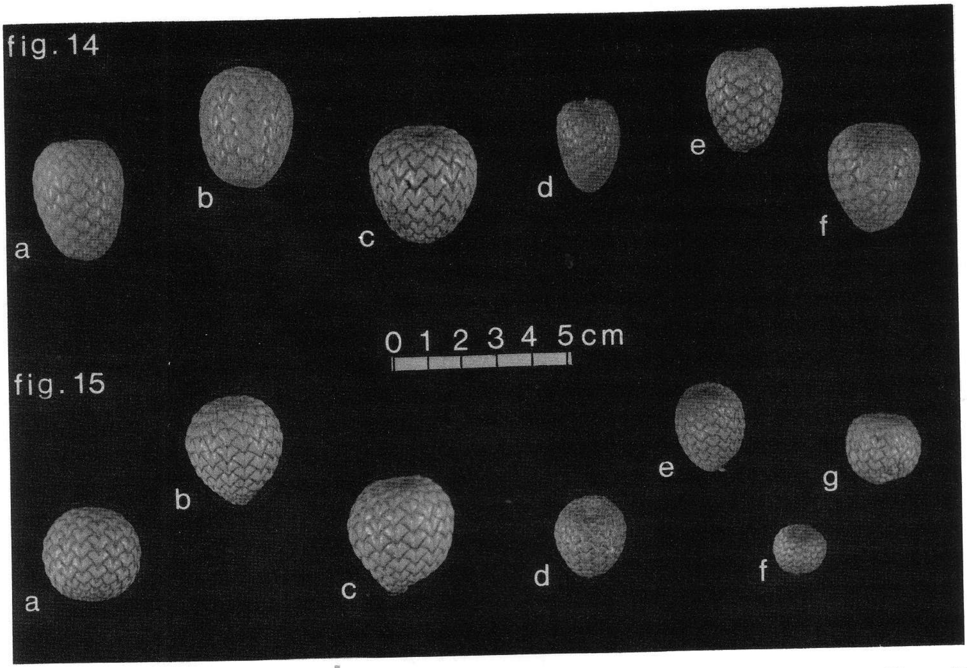
Metroxylon longispinum Martius in l.c.: 215. 18450; Miquel in l.c.: 146. 1855.

Metroxylon rumphii Mart. var. *longispinum* Beccari in l.c.: 173, p. 107. 1918. Typus: *Sagus longispina* in Herb. Amb. 1: 75. 1741.

The leaf sheath, petiole and rachis with spines that are 4–20 cm long. Bracts of inflorescence with spinules, scattered or in transverse series.

Vernacular Names: wakar, ketro, anum, ninginamé, nago, tring, passin, kangrum, wombarang, moiap.

Specimens Examined: NEW GUINEA. Malalaua, 1966, *Graven & Schodde 944* (fl., A, L), *Graven & Schodde 945* (fl., A, L); 1938, *Meyer Drees 378* (fl., fr., BO); Sepik, 1981, *Rauwerdink 100* (fr., WAG), *Rauwerdink 101* (fl., WAG), *Rauwerdink 102* (fr., WAG), *Rauwerdink 104–106* (veg., WAG), *Rauwerdink 107* (pfl., WAG), *Rauwerdink 108* (veg., WAG), *Rauwerdink 110* (veg., WAG), *Rauwerdink 111* (pfl., WAG), *Rauwerdink 113* (fr., WAG), *Rauwerdink 117* (veg., WAG), *Rauwerdink 120* (veg., WAG), *Rauwerdink 121* (fl., WAG), *Rauwerdink 124* (veg., WAG), *Rauwerdink 125* (veg., WAG), *Rauwerdink 126* (veg., WAG), *Rauwerdink 129* (veg., WAG), *Rauwerdink 130* (fr., WAG), *Rauwerdink 132* (fr., WAG), *Rauwerdink 133* (fl., WAG), Morobe, 1964, *Womersley NGF 19234* (pfl., fr.,



14–15. Fruit shapes and sizes, each from a single collection. Figure 14 from *Rauwerdink 112*, Figure 15 from *Rauwerdink 100*.

A, L); SOLOMON ISLANDS 1964, *Moore 9315 BSIP 4090* (fl., SIN, K). INDONESIA. Bengkalis, 1919, *Beguin 1919* (fl., fr., BO); CELEBES, 1895, *Koorders 18397* bis (veg., BO); AMBON, 1913, *Robinson 28* (pfl., L, K, P); JAVA, 1843, *Zollinger 1404* (fl., fr., B, P). PHILIPPINES. 1941, *Ebalo 999* (fl., BH); MINDANAO, 1909, *Elmer 11160* (pfl., fr., A, C, L, K, P), 1927, *Ramos & Edano 49399* (fl., fr., BO). CULTA. 1924, *Bakhuizen v/d Brink 3497* (veg., BO), *Bloembergen* s.n. (D1) (fl., BO), *Bloembergen* s.n. (VL 28) (veg., BO), 1939, *Burret 333* (fr., BO), 1952, *Moore 6095* (veg., BH), 1895, *Ridley* s.n. (fl., K).

2. **Metroxylon amicarum** (H. A. Wendl.) Beccari in Ann. Royal Bot. Gard. Calc. 12, 2: 187–192, p. 111–113. 1918; Moore et Fosberg in Gent. Herb. 8, Fasc. 6, art. 20: 438–444. 1956; Barrau in Econ. Bot. 13: 151–159. 1959.

Metroxylon amicarum (H. A. Wendl.) Becc. var. *commune* Beccari in l.c.: 188. 1918 (note: This name is a homotypical synonym, even though Beccari typified it with *Ledermann 13409*).

Sagus amicarum H. A. Wendland in Bot. Zeit. 36(8): 115. 1878. Typus: *Reichenbach* s.n. (not seen, possibly at W). Proposed neotype: *Furtado 25868* (holotype K, isotype A).

Coelococcus carolinensis Dingler in Bot. Centr. Bl. 32: 349, t. 2. 1887; Schumann & Lauterbach in Fl. D. Sch. Sudsee: 606. 1901. Typus: *Schneider* s.n. (not seen).

Coelococcus carolinense Beccari in Denkschr. K. Akad. Wiss. M. Nat. Kl. (Rechinger ed.), Wien, 84: 60, fig. 5a & d. 1913. Typus: *Beccari* s.n. (not seen).

Metroxylon amicarum (H. A. Wendl.) Becc. var. *majus* Beccari in Ann. Royal Bot. Gard. Calc. 12, 2: 188. 1918.

Typus: *Gibbons 1189* (not seen, possibly at B).

Solitary, pleonanthic palm, 6–8(20) m high, stem to 30 cm in diameter near base. Leaves ca. 6 m long, with spines. Inflorescences arising from axils of crown leaves, i.e. these not bractlike, reduced in size as in other *Metroxylon* species. Various inflorescences differing in developmental stage. Infructescence pendulous due to weight of numerous big fruits. In hermaphrodite flower, the style attains apex of anthers at anthesis, but in male flower, gynoecium much reduced to 3 connate, oblong bodies, reaching only to the base of anthers. Fruit globose to apple-shaped, broader than high, 6–9 by 5–8 cm, or higher than broad, 7–13 by 8–12 cm, covered with 24–28 longitudinal series of chestnut-brown (reddish) scales.

Distribution: Guam, Caroline-Islands.

Vernacular Names: röpung (Truk), *oj* (Ponape).

Specimens Examined: GUAM. 1914, *Nelson* s.n. (fl., A, P). CAROLINE-ISLANDS. Truk, *Fosberg 24522* (fl., fr., BH), *Krämer* s.n. (fl., B), 1947, *Wong 244* (fl., A); Ponape, 1914, *Kersting* s.n. (fl., B). CULTA. 1903, *Loher* s.n. (fr., K), 1907, *Lyon* s.n. (fr., K), 1929, *Anon.* (fl., fr., SIN), 1932, *Furtado 25868* (fl., fr., A, K), 1954, *Kiah ONO 114* (fl., BH).

3. **Metroxylon vitiense** (H. A. Wendl.) Beccari in Ann. Royal Bot. Gard. Calc. 12, 2: 185–186, p. 110. 1918; Barrau in Journ. Agr. B. Appl., 3: 32–36. 1956 et in Econ. Bot. 13: 151–159. 1959.

Sagus vitiensis H. A. Wendland in Seem. Fl. Vit.: 279, t. 80. 1865–68 et in App. to Seem. Vit.: 444 (teste Beccari); Benth. & H. in Gen. Pl. 3: 935. 1883; Drake de Cast. in Ill. Fl. Ins. Pac. 8: 323. 1886–92; Warburg in Ber. D. Bot. Ges. 14: 141. 1896.

Coelococcus vitiensis H. A. Wendland in Bonplandia 10: 199–200, 1862. Typus: *Seeman 658* (holotype K, isotype P).

Solitary, hapaxanthic palm, 5–10(15) m high, stem to 50 cm in diameter near base. Leaves 4–5 m long with slender spines, brown to chestnut-brown. Inflorescence apparently terminal, first-order branches erecto-patent, 2–2.5 m long, second-order branches pendulous, those seen by me 20 cm long. Style in male flower not exceeding the filaments, style in hermaphrodite flower as long as stamens. Fruit turbinate, yellowish-brown, about 7 cm high and 5 cm wide, with 27(28) longitudinal series of scales.

Distribution: Fiji-Islands.

Vernacular Name: songa.

Specimens Examined: FIJI-ISLANDS. 1860, *Seeman 658* (fl., K, P); Viti Levu, 1953, *Smith 9339* (fl., GH, K, L), 1969, *Tomlinson & Kuruvoli 16551* (fl., fr., BH).

4. **Metroxylon salomonense** (Warb.) Beccari in Denkschr. K. Akad. Wiss. M. Nat. Kl. (Rechinger ed.), Wien, 84: 60–62, fig. 5b & e & f & i et 7. 1913 et in l.c.: 192–193, p. 114. 1918; Barrau in Journ. Agr. Tr. B. Appl., 3: 32–36. 1956 et in Econ. Bot. 13: 151–159. 1959.

Coelococcus salomonensis Warburg in Ber. D. Bot. Ges. 14: 141, t. 10. 1896; Schumann & Lauterbach in Fl. D. Sch. Sudsee: 606. 1901. Typus: *Warburg* s.n. (fr.), (not seen, possibly B). Proposed neotype: *Kajewski 2300* (B).

Metroxylon bougainvillense Beccari in Denkschr. K. Akad. Wiss. M. Nat. Kl. (Rechinger ed.), Wien, 84: 60–62, fig. 5c & g & h & j. 1913 et in Ann. Royal Bot. Gard. Calc. 12, 2: 193–194, p. 114. 1918; Barrau in Journ. Agr. Tr. B. Appl., 3: 32–36. 1956 et in Econ. Bot. 13: 151–159. 1959. Typus: *Rechinger 4878* (fr.), (not seen, possibly W).

Solitary, hapaxanthic palm, 9–20 m high, stem up to 55 cm in diameter near base. Leaves 9–11 m long, with spines in transverse series. Inflorescence apparently terminal with first-order branches erecto-patent, 3–4 m long, second-order branches spreading but third-order branches pendulous, ca. 20 cm long. Flower bracts with greyish-silvery pubescence. Male and hermaphrodite flowers with filaments with a sharply reflexed subulate top, male flower with style not exceeding fused part of filaments, whereas in hermaphrodite flower, style not reaching beyond point of attachment of anthers. Fruit globose, depressed at apex and base, straw colored, 7–9 cm broad and 5.5–6.5 cm high, with 24–27 longitudinal series of scales.

Distribution: Papua New Guinea, Solomon Islands, Santa Cruz-Islands.

Vernacular Names: bia, nami, haesan.

Specimens Examined: PAPUA NEW GUINEA. BOUGAINVILLE ISLANDS, 1930, *Kajewski 2300* (fl., fr., B, BO, GH), 1964, *Schodde 4013 et 4013a* (fl., fr., A, L). SOLOMON-ISLANDS. 1936, *Lever* s.n. (fl., fr., K), 1964 *Moore 9317 BSIP 4091* (fl., fr., K, L, SIN), *Moore 9302* (fr., BH). SANTA CRUZ-ISLANDS. 1936, *Whitmore BSIP 1818* (fl., K, L, SIN).

5. **Metroxylon warburgii** (Heim) Beccari in Ann. Royal Bot. Gard. Calc. 12, 2: 182–184, p. 109. 1918; Barrau in Journ. Agr. Tr. B. Appl., 3: 32–36. 1956 et in Econ. Bot. 13: 151–159. 1959.

Coelococcus warburgii Heim in Bull. Soc. Bot. Fr. 50: 572, fig. 1–5. 1904. Typus: *Heim* s.n. (fr.), (not seen, possibly HAL). Proposed neotype: *Ridley 3171* (holotype SIN, isotype K).

Solitary, hapaxanthic palm, 6–7 m high, stem to 30 cm in diameter near base. Leaves ca. 3 m long, with spines in transverse ridges or series. Inflorescence apparently terminal with erecto-patent first-order branches, 1–1.5 m long, second- and third-order branches erecto-patent; adaxial sides of all pedicels glabrous. Flowers large, corolla (10 mm) twice as long as calyx and apex minutely punctate; in hermaphrodite flower style attains at least half the length of filaments; style in male flower as long as fused part of filaments. Fruit pear-shaped, seed in the upper, broader part, (4)7-12 cm high and (3.5)6–9 cm broad, with 24 longitudinal series of chestnut-brown scales.

Distribution: New Hebrides, W-Samoa.

Vernacular Names: tenebee, niu olotuma.

Specimens Examined: NEW HEBRIDES. 1964, *Moore 9319* (fl., P); MALEKULA, 1971, *Halle RSNH 6344* bis (fl., fr., A, K, L); PENTECOST ISLANDS, 1949, *MacDaniels 3011* (fr., BH). W-SAMOA. UPOLU, 1968, *Anon. 19331* (fl., K, P), *Bristol 2178* (fr., GH, K, L), *Bristol 2180* (fr., GH), 1971, *Moore 9985* (fl., fr., BH), 1978, *Moore 10396* (fl., fr., BH). CULTA. 1891, *Ridley 3171* (fl., fr., K, SIN), 1941, *Anon.* s.n. (fr., B).

Discussion

The first question to be considered is why *M. rumphii* Mart. (the spiny sago palm) should be synonymous with *M. sagu* (the spineless sago palm). My main argument against recognizing more than one species in the real sago palm is based upon personal observation and references in literature: a spiny sago palm can produce both spiny and spineless seedlings from a single inflorescence. For example Jumelle (1925) mentions this, and I have been able to verify that this situation occurs in PNG (Dreikikir area, road to Maprik, West-Sepik Prov.). The second question to be answered is why I have not upheld Beccari's taxonomy on the real sago palm which, even though not applying to a single species situation, covers a remarkable range of variability. It might not prove too hard to maintain at least some of his varieties. As can be seen in his key to the taxa (Beccari in l.c.: 160–162. 1918), Beccari divides species in the real sago palm into varieties and subvarieties on the bases of fruit characters such as size and shape. I do not agree with these distinctions because I have observed a considerable variability in fruit shape on the inflorescence of a single palm. Figures 14 to 15 represent samples of varying shapes selected from material collected in the Sepik-area. Each photograph represents a single number from my collection. I have compared my materials with type material of Beccari at the Herbarium Bogoriense and have found that a single accession collected by me may include several of Beccari's taxa. For example, *M. rumphii* Mart. var. *ceramense* subvar. *nigrum* and subvar. *platyphyllum* material both display fruits that are similar to *Rauwerdink 112* (Fig. 14). Therefore, I have to conclude that fruit shape and size cannot be useful in typifying taxa in the real sago palm. These characteres are most likely very dependent on age and location of the fruit in the infructescence.

For each part of the palm and for each developmental stage, spine characters are independent of age, and hence suitable for use in classification. It is convenient that this classification can take place nearly at ground level in the field. Furthermore a classification on spine characters offers a very clear distinction between the various forms of *M. sagu*. The taxonomic rank of the taxa in *M. sagu* should be low. The fact that a spiny palm may produce spiny and spineless seedlings indicates that it is heterozygous for this character and may produce embryos of at least two genotypes. The classification *forma* should apply to these taxa rather than variety or subvariety. The offspring of the aforementioned young palms may not be of the genotype of the mother-palm. I assume that a minimum of two genes or alleles governs spine length in its broadest sense. Such a situation can be expressed in Figure 16, which presents the genotypes of the occurring forms in this concept. The thesis is rather academic, however, and can only be tested in the field, but this is unfortunately seriously hampered by the lack of knowledge on the pollination mechanism in *Metroxylon*, and the fact that fruits are eaten by a number of animals. Not much is known for certain, but it is suspected that hornbills and fruit bats eat the fruits at various stages of development (local inhabitants Sepik-area pers. comm.). Wild boars are known to eat fruits on the ground (Rumphius 1741). Furthermore, particularly the formae *sagu*, *tuberatum* and *micracanthum*, long domesticated by man (e.g. the Sepik in PNG), are almost always cut down for starch extraction long before fruits even start to develop. In the rare cases that fruits are produced in these formae I have been unable to find seeds with a well-developed embryo and endosperm, seeds containing instead a hypertrophic cellular mass. In the taxon *longispinum* fruits do frequently develop an embryo and endo-

	AB	Ab	aB	ab
AB	L	L	L	K
Ab	L	L	K	I
aB	L	K	L	I
ab	K	I	I	S

16. Diagram presenting the possible genotypes of the formae of *M. sagu* where two genes control spine length. L, *longispinum*; K, *micracanthum*; I, *tuberatum*; and S, *sagu*.

sperm; this taxon is much less often cultivated.

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