BLUMEA 44 (1999) 1-24

# **REVISION OF DRYMOPHLOEUS** (ARECACEAE: ARECOIDEAE)

#### SCOTT ZONA

Fairchild Tropical Garden, 11935 Old Cutler Road, Miami, Florida 33156, USA

#### SUMMARY

A revision of the genus *Drymophloeus* (Arecaceae: Arecoideae: Ptychospermatinae) recognizes seven species, distributed from the Maluku Islands of Indonesia to Western Samoa. The history of the genus is reviewed. A key, species descriptions, a complete list of synonymy, a list of specimens examined, illustrations and distribution maps are provided. A phylogenetic hypothesis is provided, as well as a discussion of biogeography. The new combination *Drymophloeus hentyi* is made to accommodate a species formerly included in the genus *Ptychosperma*.

Key words: Arecaceae, Drymophloeus, Palmae, Indonesia, Malesia, Solomon Islands, systematics.

#### INTRODUCTION

That so insignificant a genus came to the attention of early European botanists in Indonesia is a serendipitous accident of history. Palms of the genus *Drymophloeus* Zipp. (Arecoideae: Areceae: Ptychospermatinae) were not economically important in the usual sense of cane, fiber, oil, or other items of trade; they had nothing to offer those who traded in pepper, nutmeg, and mace. But even Commerce was charmed by these unarmed, diminutive palms with dark green foliage and bright red fruits. These same charms continue to account for the cultivation of these palms far from their Malesian home. *Drymophloeus* has been in cultivation in England since 1877 (Watson, 1891) and in the United States and the Bahamas since 1940 (Fairchild, 1942).

Systematists are attracted to *Drymophloeus* by its close relationship to many other horticulturally important palms in the subtribe Ptychospermatinae. In a recent paper (Zona, 1999), I determined that, once the genus *Solfia* Rech. was re-instated, *Drymophloeus* is a monophyletic genus, so now is a propitious time to assess its taxonomy and systematics, natural distribution, and ecology.

### MATERIAL AND METHODS

This revision is based on herbarium holdings (at BH, BISH, BO, BRI, BSIP, FI, FTG, K, L, LAE, MAN, and NY), plants in cultivation at Fairchild Tropical Garden, and observations made during the course of field work in Irian Jaya (Indonesia), the Solomon Islands, and Western Samoa.

Herbarium specimens were consulted for morphological measurements, supplemented by observations of wild or cultivated plants. Floral measurements were made from either rehydrated dried material or pickled material. Fruit measurements were taken from pickled fruits or, as long as shrinkage was not great, dried specimens. Pollen measurements were made with a light microscope of pollen stained with fuchsin.

The many languages in Malesia, both indigenous and imported, cause some confusion in the naming of both political and geographic entities. Herein, the names of localities follow The Times Atlas of the World (9th comprehensive ed., 1994); however, for names that do not appear in the atlas (e.g., village names), the spelling of the original label is followed.

### DISTRIBUTION AND ECOLOGY

The genus *Drymophloeus* has a Malesian distribution. It is found in the Maluku Islands (Halmahera, Morotai, Buru, Obi, Sula, Seram, Ambon) and northwestern New Guinea (Doberai or Vogelkop Peninsula, including Waigeo Island, of Irian Jaya, Indonesia). It has been sighted, but not collected, on the Aru Islands (M.M.J. van Balgooy, pers. comm.) (Fig. 1). It is apparently absent from much of the remainder of the New Guinea mainland but appears on the island of New Britain and again in the Solomon Islands (Fig. 2).

The curious distribution of *Drymophloeus* in northwestern New Guinea and the Solomon Islands is not without precedent. Although large palms are frequently by-passed by collectors to the extent that distribution gaps often represent a lack of collections rather than real disjunction, such is not likely the case for *Drymophloeus*, which

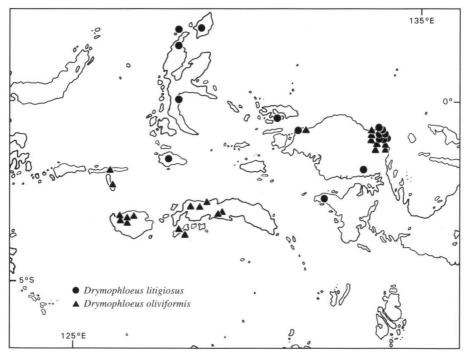


Fig. 1. The distribution of Drymophloeus in Indonesia.

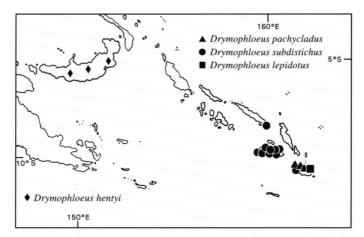


Fig. 2. The distribution of *Drymophloeus* in the Bismarck Archipelago and the Solomon Islands. *Drymophloeus whitmeeanus* of Western Samoa is not shown.

in New Guinea is usually small and relatively easy to collect. Hay (1984) noted that the fern *Christensenia* Maxon (Marattiaceae), among others, has a distribution similar to that of *Drymophloeus*.

Drymophloeus is scattered through several of the islands that make up the Solomon Islands (Fig. 2). Specimens of Drymophloeus are known from San Cristobal (Makira), Santa Isabel, Guadalcanal, and Florida Islands. Dennis & McQueen (1989) reported that the genus occurs on Malaita, Choiseul, and even Rennell Island, but I have seen no specimens from these areas. If its known distribution in the Solomon Islands is not an artifact of poor collecting, then its distribution is inexplicably patchy, by-passing several large islands with apparently suitable habitat.

The easternmost land-fall for the genus is in Western Samoa, where a species was collected only once in the early 1900s. Moore (1969) and Uhl & Dransfield (1987) suggested that *Drymophloeus* may occur on Fiji, but this possibility has not yet come to pass.

The species of Drymophloeus appear to fall into two ecological groups: the understory species of Indonesia and New Guinea, and the emergent species of the Solomon Islands. The ecology of D. whitmeeanus of Western Samoa is not known. The Indonesian and New Guinea species are D. oliviformis, D. litigiosus, and D. hentyi. These species are understory palms found in wet, swampy forests as well as in well drained hillside rain forests at a wide range of elevations (10–1200 m). These species are generally found over limestone. Drymophloeus oliviformis and D. litigiosus occur sympatrically in some areas of Irian Jaya.

The emergent species are *D. subdistichus*, *D. pachycladus*, and *D. lepidotus*. The first two species may be found in secondary growth and open forests over limestone up to 600 m elevation (Dennis & McQueen, 1989). *Drymophloeus lepidotus* was reported by Moore (1969) to occur on ultrabasic hills at 430-490 m (1400-1600 ft).

The lands presently occupied by *Drymophloeus* are Gondwanic in origin (Audley-Charles, 1981). The Maluku Islands, northwestern New Guinea, New Britain, and the Solomon arc have been separate since at least Eocene times, although it is unlikely that all of these land areas have had a continuous history of emergence during that time. In fact, the Florida Islands, Guadalcanal, San Cristobal, and Santa Isabel are islands of limestone and volcanic sediments laid down in Miocene times (Ridgeway, 1987). Northwestern New Guinea, where *D. oliviformis* and *D. litigiosus* are sympatric, is an area of either primary or secondary contact; the biogeographic evidence is equivocal, and this question remains unresolved. Their present distribution, coupled with the fact that these palms have red, fleshy fruits attractive to birds, suggests that both over-water dispersal and vicariance have played a role in the historical biogeography of these species.

### MORPHOLOGY

### Roots

The roots of *Drymophloeus* are adventitious, stout, and brown to gray in color. In *D. oliviformis* and *D. litigiosus*, stilt or prop roots are typically present (Fig. 3a), although they may not form in cultivation. The stilt roots form a cone up to 100 cm high, and they may be branched. They often bear linear rows of pneumathodes that are visible as small, light, corky emergences longitudinally arranged on the otherwise smooth surface of the root.

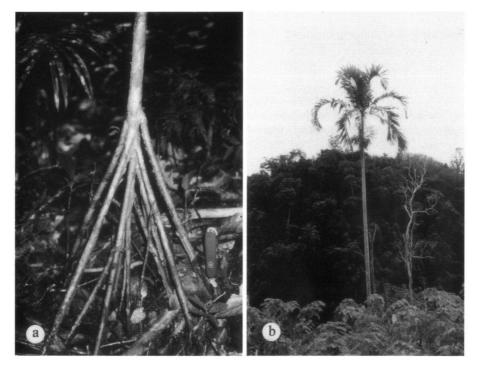


Fig. 3. a. Stilt roots of *Drymophloeus litigiosus*; b. the tall, ringed stem of an emergent species, in this case *D. subdistichus* in Guadalcanal, Solomon Islands.



Fig. 4. a. Caespitose individual of *Drymophloeus oliviformis*; b. *D. oliviformis* infructescence. Note that fruits are not borne on the distal portions of the rachillae, as these areas bore only staminate flowers.

### Stem

In the understory species of *Drymophloeus*, the stem is slender, 1.3-8 cm diam., with widely spaced, conspicuous leaf scars. In the emergent species, the stem is thicker (7.5-35.6 cm diam.), brown or gray with vertical fissures, and leaf scars that become less conspicuous with age (Fig. 3b).

One population of *D. oliviformis* from low, swampy forest in Irian Jaya (represented by *Zona et al. 687*) was found to comprise weakly caespitose individuals (Fig. 4a). Likewise, one population of clustering *D. litigiosus* is known (represented by *Davis et al. 723*). While the caespitose condition is unusual in *Drymophloeus*, it is certainly not startling. Many Ptychospermatinae are caespitose, and this character is highly labile, sometimes even dependent on environmental or horticultural conditions. The genetic basis for multiple stems is not known but may be as simple as a single gene. Caespitose individuals of *Drymophloeus* do not deserve formal taxonomic recognition.

The outer cortex of *Drymophloeus* species is fibrous and hard, often densely packed with hard, black fibers, surrounding a soft and pithy inner cortex. I have observed that *Drymophloeus* wood (probably *D. pachycladus*) is used for the construction of bows in the Florida Islands of the Solomon Islands. Other collectors have noted that the wood from *D. pachycladus* and *D. subdistichus* is used for flooring and siding.

#### Leaves

The leaves of *Drymophloeus* are alternate and spirally arranged and are pinnately divided. The leaf segments are sometimes described as having a rubbery texture. In understory species, they may have a metallic sheen, and emerging leaves may be reddish. The leaves have sheathing leaf bases that form a distinct, tubular crownshaft (a cylinder borne at the apex of the stem), and they may be petiolate. The sheaths are covered to varying degrees with silvery, branched, multicellular trichomes. At the apex of the sheath and along the petiole and rachis, dark brown or black ramenta are present, again to varying degrees. The degree of pubescence appears to be highly variable and is given little taxonomic weight.

It may be said in general that understory palms are more variable in vegetative features than emergent (full-sun) palms, and this rule of thumb applies all too well to *D. oliviformis* and *D. litigiosus*. The confounding plasticity in leaf segment shape and size led to the over-description of species, most of which can now be assigned to these two understory species. Segments vary from narrow and linear to broadly flabellate. Thus, segment shape is useless in delimiting species, and species historically recognized by leaf segment shape cannot be maintained. The surprising variability of segment shape continues to bedevil botanists and horticulturists to this day.

The terminal segments of a *D. oliviformis* leaf are often united to form a single, flabellate segment. In contrast, *D. litigiosus* has broad but distinct terminal segments. Unfortunately, this useful distinguishing feature is not always reliable in that some specimens of *D. oliviformis* (e.g., *Van Royen 3160, Zona et al.* 668) have a slightly cleft or divided terminal segment. However, the united terminal segment feature is unique to *D. oliviformis* and, when present, is a reliable character for identifying sterile specimens. *Drymophloeus hentyi* and the Solomon Islands species have distinct terminal segments that are narrower, not broader, than the penultimate segments.

Leaf segment apices in Drymophloeus are erose and sinuate. This feature is useful at the generic level in distinguishing Drymophloeus from related genera, such as Ptychosperma, but is shared with Balaka and Solfia (Zona, 1999).

Venation in *Drymophloeus* leaf segments consists of a strong midvein and numerous secondary and tertiary veins. Marginal veins are present, but conspicuous cross veins are not. Leaf blades may possess ramenta along the abaxial surfaces of the midveins and at the base of each segment on the abaxial side. Leaf rachises are clothed in brown, scaly tomentum to varying degrees.

### Inflorescence

The inflorescence in *Drymophloeus* is infrafoliar, one per node, and is green in color. It is enclosed by a prophyll, which is either persistent or caducous, depending on the species. When it abscises, the prophyll develops a longitudinal split on the abaxial or adaxial side. The single peduncular bract, attached to the peduncle well above the prophyll, pierces the prophyll during its growth and elongation. An incomplete, second peduncular bract, attached above the first, is also present. At maturity, the peduncular bract usually splits longitudinally on the abaxial side, or laterally, and either falls away or is persistent, depending again on the species. Persistent prophyll and peduncular bract are characteristic of *D. litigiosus* and *D. oliviformis*. Small, insignificant bracts subtend branches and rachillae.

The peduncle in *Drymophloeus* is long, usually one and one-half to two times as long as the remaining portion of the inflorescence. The exception is *D. subdistichus*, in which the peduncle is less than one-half the length of the rachillae-bearing portion of the inflorescence. The angle formed by the inflorescence and the trunk was thought by Dennis & McQueen (1989) to be a significant species-level character. I do not believe that it is. The species illustrated by them (1989: 18) as *Drymophloeus* sp. 'Nggela' is none other than *D. pachycladus*.

Inflorescences have two to four orders of branching (sensu Tomlinson, 1990). Those of *D. pachycladus* and *D. oliviformis* are the most sparsely branched; while *D. sub-distichus* and *D. lepidotus* have the most branched inflorescences. Pistillate flowers may be borne throughout or only basally. They are often arranged spirally at the base of the rachillae but are distichously or subdistichously arranged distally. This arrangement is most clearly seen once the fruit develop. It is the reason for the epithet of *D. subdistichus*, but I have seen distichously arranged fruit in *D. oliviformis* (*Bloembergen* 4467), *D. litigiosus* (*Anonymous s. n.* – BO), and *D. pachycladus* (*Powell BSIP* 19361). Moore (1969) noted subdistichously arranged flowers in *D. lepidotus*.

The prophyll and peduncular bracts possess a silvery tomentum of multicellular, branched trichomes, with dark ramenta often present toward the apices. The inflorescence itself may be public to varying degrees with multicellular, branched, brownish trichomes.

Like all Ptychospermatinae, the inflorescence of *Drymophloeus* is exposed from the bracts well before anthesis begins. The lag time between bract dehiscence and anthesis may be as long as two or three months.

Inflorescences of *Drymophloeus* are strongly protandrous. At the time of staminate anthesis, pistillate flowers are often little more than immature buds on the inflorescence. The flowers appear to have some of the characteristics of a bee pollination syndrome (protandry, diurnal flowering, copious pollen production, flowers light-colored), and indeed, *D. pachycladus* in cultivation at FTG is visited by Halictid bees.

### Flowers

The flowers are arranged in triads of one pistillate flower flanked by two staminate flowers, although only staminate flowers may be borne along the distal portions of the rachillae. Each triad is subtended by a small, crescent-shaped bract, and each staminate flower is also subtended by a minute bract. The bracts and abaxial surfaces of the sepals and petals may be pubescent with small, branched, brownish trichomes to varying degrees.

Staminate flowers have three free sepals, imbricately arranged in the characteristic 'arecoid' fashion: one sepal with both margins outside all the other sepals, one sepal with both margins in or enclosed, and the third sepal with one margin in and one out. Sepals are semi-orbicular to reniform, with hyaline and minutely fimbriate margins. They are strongly keeled and cochleariform. Petals are three, free or sometimes basally adnate to the stamens, and valvate. They are greenish-white to yellowish or even brownish or reddish in life. The stamens are many, up to more than 300, arranged in several whorls. The pistillode is lageniform or ovoid to spheroid and trifid, and is longer or shorter than the stamens. The flowers have no detectable fragrance.

Pollen of those species investigated is ellipsoidal, monosulcate with a finely reticulate exine, characteristics that are unremarkable within the Areceae. Thanikaimoni (1971) found that the grains of *Drymophloeus oliviformis* are  $58-60 \,\mu\text{m}$  long, whereas those of *D. pachycladus* (as *Rehderophoenix pachyclada*) are larger,  $60-65 \,\mu\text{m}$  long. I also found that *D. oliviformis* and *D. litigiosus* have smaller pollen than *D. subdistichus* and *D. pachycladus* (Table 1).

Pistillate flowers also have three sepals and three petals, but both are imbricately arranged, with hyaline and minutely fimbriate margins. The petals are green, yellowish, or white in life. The apices of petals are thickened and valvate. The staminode is present as three lobes of tissue, less than 1 mm long, and inconspicuous. The ovary is superior, ovoid to cylindrical, and without a style. The stigma is trifid and papillose. The flowers lack fragrance.

Read (1966) determined that n = 16 for *Drymophloeus litigiosus* (as *D. beguinii*). This number is the most common number in the Arecoideae (Uhl & Dransfield, 1987).

species	voucher	n	range	mean
D. litigiosus	Read 1395	15	29.3-38.3	32.6
D. litigiosus	Hill 2631	15	33.8-42.8	38.7
D. oliviformis	Zona 605	15	31.5-42.8	37.7
D. pachycladus	Zona 486	15	38.3-47.3	42.9
D. pachycladus	Zona 766	15	42.8-49.5	46.4
D. subdistichus	Zona 641	15	45.0-56.3	49.5

Table 1. Pollen lengths (longest axis) for selected species of *Drymophloeus*. All values are in micrometers ( $\mu$ m). Vouchers are deposited at FTG.

# Fruits and seeds

Drymophloeus fruits are drupes, which ripen from green through yellow to red (Fig. 4b). They are ellipsoidal, sometimes nearly cylindrical, obovoid, or fusiform (especially when dry). The stigmatic scar is apical and prominent. They are juicy, raphide-containing, and are often reported to cause dermatitis, although sensitivity to Drymophloeus irritants varies from person to person. When dry, the exocarp may appear finely rugose as the result of fiber ends visible just under the surface. The endocarp is straw-colored and finely fibrous. The interior of the endocarp is vitreous and caramel-colored or black.

Seeds are ovoid, cylindrical, or even spheroidal, with a shallow raphe running the length of the seed from which radiate shallowly impressed fibers. The hilum is apical and small. The endosperm is homogeneous or runniate, and this character is superbly useful in differentiating the very similar *D. oliviformis* and *D. litigiosus*.

### PHYLOGENETIC RELATIONSHIPS

Recent phylogenetic studies of the subtribe Ptychospermatinae showed Drymophloeus s. l. to be polyphyletic and paraphyletic (Zona, 1999). Drymophloeus samoensis was shown to be unrelated to the 'core' Drymophloeus and was returned to the genus Solfia by Zona (1999). Ptychosperma hentyi, despite having shallow lobes on its endocarp, exhibits all the synapomorphies of Drymophloeus s. s. and is herein transferred to Drymophloeus. The cladistic analysis (Zona, 1999) provided equivocal evidence for splitting *Drymophloeus* (understory palms) and *Rehderophoenix* (emergent palms). Until definitive evidence comes to hand showing that these two lineages should be segregated, I shall continue to recognize both taxa as forming *Drymophloeus s. s.* 

Drymophloeus is thereby characterized by having cuneate to elongate leaf segments with apices that are erose-sinuate, a long peduncle relative to the remainder of the inflorescence (except in *D. subdistichus*), green inflorescence axes, pistillodes either longer or shorter than the stamens, and finely fibrous, straw-colored endocarps.

Drymophloeus is phylogenetically close to Brassiophoenix, Balaka, and Solfia, all of which share the cuneate to elongate leaf segments, elongate peduncle, and green inflorescence axes. My analysis identified Balaka as the closest sister group to Drymophloeus (Zona, 1999).

Within the genus *Drymophloeus*, relationships were analyzed by maximum parsimony analysis using Hennig86 version 1.5, with the ie and bb options (Farris, 1988). Analysis of 11 characters (Table 2) polarized with *Balaka seemannii* (H. Wendl.) Becc. (Table 3) yielded a single, most-parsimonious tree (Fig. 5) of 13 steps. Regrettably, the poorly known *D. whitmeeanus* could not be included in the analysis.

Table 2. Characters used in the cladistic analysis of the species of *Drymophloeus*. The characters are polarized according to the condition found in the outgroup, *Balaka*. The plesiomorphic condition is scored as zero; the apomorphic condition as one. See text and Zona (1999) for explanation of characters. Noninformative autapomorphies are excluded from the analysis.

1.	stilt roots $absent = 0$ ; present = 1
2.	understory palm = 0; canopy emergent palm = 1
3.	prophyll persistent = 0; caducous = 1
4.	peduncular bract caducous = 0; persistent = $1$
5.	stamens $< 100 = 0; > 125 = 1$
6.	pistillode longer than the stamens = $0$ ; as long or shorter = $1$
7.	endocarp fibers brown = 0; straw-colored = $1$
8.	endocarp fibers thick = 0; hair-like = $1$
9.	endocarp angled = 0; terete = 1
10.	endocarp without ridge = 0; with ridge = $1$
11.	endosperm homogeneous = 0; ruminate = 1

Table 3. Data matrix for analysis with Hennig86. The species are identified by their epithets; the outgroup is *Balaka*. Note that *Drymophloeus whitmeeanus* is so poorly known that it was omitted.

-	1	2	3	4	5	6	7	8	9	10	11
outgroup	0	0	0	0	0	0	0	0	0	0	0
hentyi	0	0	1	0	0	1	1	1	1	0	1
litigiosus	1	0	0	1	0	1	1	1	1	0	1
lepidotus	0	1	1	0	0	1	1	1	1	0	0
oliviformis	1	0	0	1	0	0	1	1	1	0	0
pachycladus	0	1	1	0	1	1	1	1	1	1	0
subdistichus	0	1	1	0	1	1	1	1	1	1	0

Drymophloeus subdistichus and D. pachycladus, formerly of the genus Rehderophoenix, form a monophyletic group nested within Drymophloeus. Moore's (1969) decision to include Rehderophoenix within Drymophloeus is fully supported. Likewise, D. hentyi, formerly placed in Ptychosperma, is clearly part of Drymophloeus.

The phylogenetic hypothesis illustrated in Figure 5 agrees strongly with geographic distributions of the taxa. The two Indonesian taxa, *D. oliviformis* and *D. litigiosus*, are shown to be sister species. Likewise, the three Solomon Islands taxa are sister species. *Drymophloeus hentyi* of the Bismarck Archipelago, in the middle of the cladogram, is geographically intermediate as well.

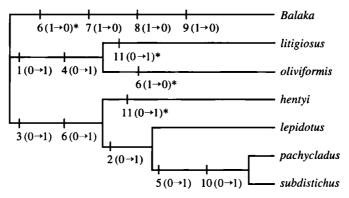


Fig. 5. The single most parsimonious tree resulting from the cladistic analysis of the genus *Drymophloeus*. Homoplasy is indicated with an asterisk (\*). CI = 0.84; RI = 0.80. Length (number of steps) = 13. Autapomorphies are excluded.

#### TAXONOMIC HISTORY

Palms now known as *Drymophloeus* first came under the scrutiny of one of the foremost pre-Linnean botanists and collectors in the Malesian region, Rumphius. His illustration of '*Saguaster minor*' was the first illustration of a *Drymophloeus* and eventually became the type of *D. oliviformis*. With the publication of Herbarium Amboinensis in 1741–1750, Rumphius' palms came to the attention of European botanists, who began assigning binomials to Rumphian taxa with almost carefree abandon.

The genus Drymophloeus was not established until 1829 when Alexander Zippelius proposed the genus in a published letter to Blume. The letter was written near the coast of Timor shortly before his death and dated 9 October 1828 (Beccari, 1885). Zippelius reported that he made three collections of this new genus, which he likened to *Iriartea* (probably because of the broadly flabellate leaf segments and stilt roots). He also found a resemblance to *Caryota* in both the praemorse leaf segment apices and urticating mesocarp of the single-seeded fruit. The seed, Zippelius noted, had a homogeneous endosperm, a characteristic of the species now known as *D. oliviformis*. Two undated collections by Zippelius are present in the herbarium at Leiden, one of which bears the name '*Iriartea monogyna*'. It is unclear whether '*Iriartea monogyna*' was proposed before Zippelius wrote to Blume, or Zippelius changed his mind on his

new genus and decided to force the species into *Iriartea*. The name '*Iriartea monogyna*' was subsequently published by Macklot, but the name is a nomen nudum (Henderson, 1990).

Some botanists equated *Drymophloeus* with genera such as *Caryota, Pinanga, Actinokentia, Harina* (= *Wallichia*), and assorted genera in the Ptychospermatinae. A number of new taxa were described in or transferred to the genus *Drymophloeus* by Miquel, Martius, and others. Some names, as a result of a lack of type specimens, are per force relegated to the category of nomina confusa et ambigua(see Excluded Names).

Odoardo Beccari devoted considerable attention to Drymophloeus and its relatives, although his generic concept evolved during the course of his life. His first foray into Drymophloeus occurred when he published descriptions of taxa he collected in northwestern New Guinea (Irian Jaya, Indonesia) in the early 1870s (Beccari, 1877a & b). At that time, he included in Drymophloeus those species he later treated as Actinophloeus and which are now treated as Ptychosperma. In 1885, he considered the palms growing in Buitenzorg, which had previously been interpreted by Scheffer (1876). Beccari (1885) limited to five the number of species in Drymophloeus, and treated many names as synonyms or as taxa belonging to other genera, including Coleospadix, a genus erected by Beccari in the same publication. In 1935, Martelli published Beccari's posthumous checklist of Areceae, in which the monotypic Solfia, erected in 1907 by Rechinger, was included within Drymophloeus. In Beccari's last posthumous word on the subject, Beccari & Pichi-Sermolli (1955) treated Drymophloeus in depth, recognizing as subgenera taxa now treated as Balaka and Solfia. Coleospadix and Rehderophoenix (described by Burret in 1936) were treated separately.

Harold E. Moore, Jr. gave *Drymophloeus* its modern circumscription in 1953, when he united *Coleospadix* with *Drymophloeus*, and in 1969, when he sank *Rehderophoenix*. The generic concept of Moore was followed by Uhl & Dransfield (1987). Only recently (Zona, 1999) has *Solfia* been removed from *Drymophloeus*. The genus, thus modified, appears to be monophyletic and natural.

The meaning of the generic name was not explained by Zippelius. Moore (1958) believed the name to be derived from the Greek words *drymos* (a wood or forest) and *phloios* (bark), a combination that makes little sense ("bark of the forest"?). I believe Zippelius had in mind *drymos* and *phleos* (a marsh reed), in reference to the thin, reedy stems of this forest understory palm (*D. oliviformis*).

### DRYMOPHLOEUS

- Coleospadix Becc., Ann. Jard. Bot. Buitenzorg 2 (1885) 90. Type species: C. litigiosa (Becc.) Becc. = D. litigiosus (Becc.) H.E. Moore.
- Saguaster Kuntze, Revis. Gen. Pl. (1891) 734. Type species: S. oliviformis (Giseke) Kuntze = D. oliviformis (Giseke) Miq.
- Rehderophoenix Burret, Notizbl. Bot. Gart. Berlin-Dahlem 13 (1936) 86. Type species: R. pachyclada Burret = D. pachycladus (Burret) H.E. Moore.

Solitary, rarely weakly caespitose, emergent or understory, pleonanthic (not dying after flowering, i.e., growing and flowering perennially), monoecious palms. *Roots* ad-

<sup>Drymophloeus Zipp., Alg. Konst- en Letterbode 1829, 19 (8 May 1829) 297; Flora 12 (1829) 285.
— Lectotype species: D. oliviformis (Giseke) Miq. [fide Pichi-Sermolli in Webbia 11 (1955) 94].</sup> 

ventitious, brown with scattered longitudinal files of pneumathodes, sometimes forming prop or stilt roots above the soil surface. Stem erect, unbranched, 1.3-35.6 cm diam. and up to 25 m tall, green, brown, or gray with prominent leaf scars, infrequent populations of some species occasionally producing suckers; wood with numerous, hard, black, fiber-sheathed vascular bundles in the peripheral region (especially at the base of the palm) but fewer bundles embedded in a soft, light brown matrix in the center. Leaves alternate and spirally arranged, 6-15 in the crown, with prominent sheathing bases forming a crownshaft; leaf sheath 15.5-89 cm long, green to brown, with tawny or silvery multicellular scale-like trichomes throughout and blackish scale-like trichomes prominent at the apex of the sheath; petiole present or not, rounded abaxially, channeled adaxially but becoming channeled with a single longitudinal ridge distally, clothed in brownish multicellular scale-like trichomes to varying degrees, merging imperceptibly with the leaf rachis. Leaf segments subopposite, 7-39 pairs per leaf, linear to broadly cuneate or flabellate in outline, segment apex sinuate-erose, sometimes obliquely so with an attenuated leading edge, sometimes approaching a three-pronged condition (as in Brassiophoenix), plication reduplicate, terminal segments united into one single flabellate segment or not, segments with a single primary midvein (or multiple primary veins, in the terminal segments), secondary and tertiary veins numerous, along with prominent marginal veins, transverse veins obscure. Inflorescence infrafoliar, branched to the second or third order, solitary at the nodes, enclosed in a single prophyll and single peduncular bract; prophyll bicarinate, with a notched or cleft apex, caducous or persistent, with tawny or silvery multicellular scale-like trichomes throughout; peduncular bract emerging through the apex of the prophyll, causing the prophyll to split longitudinally along the abaxial or adaxial side, opening longitudinally, laterally or on the abaxial side, caducous or marcescent, with tawny or silvery multicellular scale-like trichomes throughout and blackish scale-like trichomes prominent at the apex; incomplete secondary peduncular bract present; peduncle green, long [relative to the branched portion of the inflorescence (except D. subdistichus)], glabrous or pubescent with dark brown scurfy scales; rachillae green, pubescent or not, exposed for a long time prior to anthesis. Flowers imperfect, borne in triads of 1 pistillate flower flanked by 2 staminate flowers, subtended by minute bracteoles; staminate flowers borne in pairs or singly in distal portions of the rachillae; flowers distichous (at least distally), subdistichous, or spirally arranged on the rachillae. Staminate flowers sessile, sepals 3, free, imbricate with 'arecoid' aestivation (1 sepal with both margins out, 1 with both in, 1 with one margin out and one in), reniform or semi-orbicular, strongly keeled, margins hyaline, minutely and sparsely ciliate; petals 3, sometimes partially adnate to the stamens at their bases, valvate, ovate, margins entire; stamens 24-320 in many whorls, filaments awl-shaped, anthers linear, with subequal sacs and sometimes with basal lobes divergent, dorsifixed and versatile; connective darkly pigmented; dehiscence latrorse; pistillode lageniform and longer than the stamens, or ovoid to globose or trifid and shorter than the stamens. Pistillate flowers sessile, sepals 3, free, imbricate, reniform or semi-orbicular, margins hyaline and erose-fimbriate; petals 3, free, imbricate basally but valvate at the tips, semi-orbicular, margins hyaline and erose-fimbriate but thick at the tips; staminode present as 3 flaps of tissue at the base of the ovary; gynoecium of 3 connate carpels but pseudomonomerous, globose, glabrous; style absent; stigma three-lobed, dry. Fruit drupaceous, ovoid to fusiform,

fleshy, ripening from green to yellow to red, borne in the cupule of the enlarged and coriaceous to cartilaginous perianth parts, stigmatic remains apical, exocarp smooth in life but often finely pebbled when dry, mesocarp watery, with few fibers, sometimes containing abundant raphides, endocarp terete in cross section (sometimes five-lobed in *D. hentyi* and *D. subdistichus*), finely fibrous, straw-colored, netted externally, chartaceous internally, the inner wall of the endocarp caramel-colored, brown, or black, vitreous. Seed spheroid to ellipsoid, hilum apical, raphe reticulate; endosperm homogeneous or ruminate; embryo minute, basal. Germination adjacent-ligular; *eophyll* bifid with erose apices or entire and ovate with erose margins.

# KEY TO THE SPECIES

1a.	Fruits more than 30 mm long 7. D. whitmeeanus
b.	Fruits equal to or less than 30 mm long 2
	Endosperm ruminate
	Endosperm homogeneous
3a.	Stilt roots sometimes present, interior of endocarp caramel-colored; seed terete
b.	Stilt roots absent, interior of endocarp shiny black, seed usually slightly lobed
	1. D. hentyi
4a.	Emergent palms, terminal leaf segments not united, prophyll and peduncular bract
	caducous, pistillode shorter than stamens
b.	Understory palms, terminal leaf segments usually united into a single flabellate
	segment, prophyll and peduncular bract persistent, pistillode longer than stamens
	4. D. oliviformis
5a.	Stamens more than 150, endocarps with a single flattened ridge on one side . 6
b.	Stamens fewer than 100, endocarp terete, lacking a flattened ridge
6a.	Peduncle longer than rachillae-bearing rachis of inflorescence; inflorescences
	branched to 2 orders 5. D. pachycladus
b.	Peduncle shorter than rachillae-bearing rachis, inflorescence branched to 3 or 4
	orders 6. D. subdistichus

### 1. Drymophloeus hentyi (Essig) Zona, comb. nov.

Ptychosperma hentyi Essig, Principes 31 (1987) 113. — Type: Papua New Guinea, West New Britain Province, Kandrian Subprovince, along west side of Pulie River, Henty & Frodin NGF 27237 (holo LAE; iso BH).

Solitary, understory palm bearing 10(-13) pendant leaves. *Stem* 5-8(-10) m tall, 6-8 cm diam.; stilt roots absent. *Leaf* 157-261 cm long; petiole 15-21 cm long; sheath 45.5-75 cm long; 12-21 pairs of segments, middle segment 29-54 cm long, 9.5-30 cm wide, cuneate; terminal segments not united. *Inflorescence* c. 75 cm long; prophyll 14-27.5 cm long, 1.3-3 cm wide; peduncular bract 9-24.5 cm long, c. 4.5 cm wide; peduncle 12-17 cm long; rachillae 110-200 mm long, c. 1.5 mm diam. (at base), with 7-9 pistillate flowers per 5 cm. *Staminate flower* 6-7(-10) mm long, c. 3.8 mm diam.; sepals reniform to semi-orbicular, c. 2.9 mm long, 4 mm wide; petals linear-elliptical,

c. 5.4 mm long, 3 mm wide; stamens 25–36, c. 3 mm long; filament c. 1.5 mm long; anther c. 2.5 mm long, c. 0.4 mm wide; pistillode conical, 0.3–2 mm long, style absent. *Pistillate flowers* not seen. *Fruit* red when ripe, broadly fusiform to nearly globose, fleshy and juicy, 15–16.1 mm long, 9–13 mm diam.; exocarp slightly striate when dry; endocarp fusiform, inner wall black, vitreous, 15–15.6 mm long, 9.6–10.3 mm diam.; *seed* globose or slightly oblate spheroid, sometimes weakly to strongly five-lobed, brown, 7.8–9.1 mm long, 7.5–8.3 mm diam.; endosperm ruminate. *Eophyll* bifid, apical margins erose.

Common names --- None recorded.

Distribution — Known only from the island of New Britain, at 0-670 m elevation (Fig. 2). Occasionally cultivated outside its native range.

Notes — The above description relies heavily on the original description by Essig (1987), supplemented by observations taken from additional specimens and living material in cultivation.

This species was originally described in the genus *Ptychosperma* because of its (sometimes obscurely) lobed endocarps. Examination of the endocarps of *D. subdistichus* revealed that they are also obscurely lobed at the apex of the endocarp, so *D. hentyi* is not unique in the genus in possessing lobed endocarps. Endocarp lobing has evolved several times in the Ptychospermatinae (Zona, 1999); hence, it cannot be used as the sole criterion for identification at the generic level.

Although few specimens exist, illustrations of this palm (as Drymophloeus sp., Ptychosperma sp., or Ptychosperma hentyi) were published in Hay (1984) and Essig (1987, 1995).

#### 2. Drymophloeus lepidotus H.E. Moore

Drymophloeus lepidotus H. E. Moore, Principes 13 (1969) 75, 76. — Type: British Solomon Islands Protectorate, San Cristobal: ultrabasic hill east of Wainoni, 10 Aug. 1965, *Dennis 53* (holo BH; iso BSIP, K, L, LAE).

Solitary, emergent palm. Stem c. 9 m tall, 7.5-10 cm diam.; stilt roots absent. Leaf sheath not seen; middle leaf segment 41-54.5 cm long, c. 4.6 cm wide, linear-cuneate; terminal segments not united. Prophyll c. 29 cm long, c. 2.5 cm wide, caducous; peduncular bract c. 33 cm long, c. 4.5 cm wide, caducous; peduncle 10-11 cm long, 1.4-1.6 cm wide; rachillae more than 10, c. 190 mm long, c. 2.4 mm diam., with 9-12pistillate flowers per 5 cm. Staminate flower 4.4-4.8 mm long, 2.8-3.1 mm diam.; sepals reniform to semi-orbicular, 2.2-2.6 mm long, 2.8-3.3 mm wide; petals ovate, creamy white, 3.6-4.3 mm long, 2.7-3.2 mm wide; stamens 34-45, c. 3.2 mm long; filament c. 1.5 mm long; anther 1.9-2.5 mm long, 0.4-0.5 mm wide; pistillode 1.9-2.2 mm long, 0.3–0.4 mm diam., style present. *Pistillate flowers* borne proximally on the rachillae, spirally or subdistichously arranged; not seen. Fruit red when ripe, elongate ovoid, fleshy and juicy, 23.5-25.7 mm long, 9.3-10.5 mm diam.; exocarp finely rugose when dry, fiber ends visible; endocarp fusiform, bearing a single flattened ridge on one side, inner wall shiny ochre in color; seed ellipsoid to ovoid, flattened at the base, brown, 14.1–15.8 mm long, 7.2–7.8 mm diam.; endosperm homogeneous. Eophyll not seen.

Common names — None recorded.

Distribution — Known only from the island of San Cristobal, Solomon Islands, at 430–490 m elevation (Fig. 2).

Notes — This species is known only from the type collection and from Moore's (1969) detailed description. I have no new observations to add to his.

### 3. Drymophloeus litigiosus (Becc.) H.E. Moore

- Drymophloeus litigiosus (Becc.) H.E. Moore, Principes 13 (1969) 76. Ptychosperma litigiosum Becc., Malesia 1 (1877) 50 ('litigiosa'). — Coleospadix litigiosa (Becc.) Becc., Ann. Jard. Bot. Buitenzorg 2 (1885) 90. — Type: New Guinea, Andai, 1872, Beccari 511bis (holo FI-W).
- Drymophloeus oninensis (Becc.) H.E. Moore, Principes 13 (1969) 76. Ptychosperma litigiosum var. oniensis Becc., Malesia 1 (1877) 52. Coleospadix oniensis (Becc.) Becc., Ann. Jard. Bot. Buitenzorg 2 (1885) 90. Saguaster oninensis (Becc.) Kuntze, Revis. Gen. Pl. (1891) 735. Type: New Guinea. Kapaor, Apr. 1872, Beccari 59 (holo FI-W).
- Drymophloeus beguinii (Burret) H.E. Moore, Gentes Herb. 8 (1953) 304. Coleospadix beguinii
   Burret, Feddes Repert. Spec. Nov. Regni Veg. 24 (1928) 286. Type: Molucca Islands,
   Halmahera Island: Weda, 1 Feb. 1923, Beguin 2347 (holo B, destroyed; iso BO; photo BH).
- Drymophloeus porrectus (Burret) H.E. Moore, Gentes Herb. 8 (1953) 307. Coleospadix porrectus Burret, Feddes Repert. Spec. Nov. Regni Veg. 24 (1928) 287. — Type: Molucca Islands, Halmahera Island; Galela, Soa Tobaroe, 23 Dec. 1921, Beguin 1930 (holo B, destroyed; iso BO; photo BH).

Solitary or weakly caespitose understory palm bearing 7-9 leaves. Stem 1-6 m tall, 1.3-5 cm diam.; stilt root cone 30-100 m tall. Leaf 114-300 cm long; petiole 22-48cm long; sheath 20-79.5 cm long; 7-16 pairs of segments, middle segment 23-64 cm long, 4.3-20.5 cm wide, linear-lanceolate to broadly flabellate, borne 6-12.5 cm apart; terminal segments not united. Inflorescence 47-75 cm long; prophyll 14-28(-51) cm long, 1.3-3 cm wide, persistent; peduncular bract 17.5-41.5 cm long, 1.1-2.5 cm wide, dehiscing along the abaxial or adaxial side, green and persistent; peduncle 13.5-37.5 cm long, 0.3-1.2 cm wide; rachillae 6-22, 120-400 mm long, 1-3.3 mm diam., with (6-)12-16 pistillate flowers per 5 cm. Staminate flower 4.2-6.2 mm long, 2-3 mm diam., greenish to reddish brown in bud; sepals reniform to semi-orbicular, 1.7-2.7 mm long, 2–2.6 mm wide; petals linear-elliptical to linear-ovate, greenish brown, 3.3-5.6 mm long, 1.2-2.7 mm wide; stamens 24-32, 2.9-4.2 mm long; filament 1.8-3 mm long; anther 1.5-2.1 mm long, 0.3-0.4 mm wide; pistillode 1.6-3.7 mm long, 0.6–1.3 mm diam., style absent. *Pistillate flowers* borne proximally or throughout the length of the rachillae, spirally arranged, sometimes distichously arranged distally, greenish or reddish brown, 2.5-5.4 mm long, 3.3-4.2 mm diam.; sepals semi-orbicular, 2.2-2.6 mm long, 2.9-3.9 mm wide; petals semi-orbicular to reniform with cuspidatevalvate apices, 2.3-4.2 mm long, 2.4-5.1 mm wide; gynoecium conical, 2-3.8 mm long, 0.7-1.7 mm diam. Fruit red when ripe, fusiform to ovoid or obovoid, fleshy and juicy, 13.6–23.4 mm long, 5.8–11.1 mm diam.; exocarp smooth or slightly striate or finely rugose when dry, fiber ends visible; endocarp fusiform, inner wall caramelcolored, 15.2-16.2 mm long, 7-8.1 mm diam.; seed globose, sometimes flattened at the base, brown, 7.4–13.5 mm long, 3.5–8.6 mm diam.; endosperm ruminate. Eophyll elliptical, notched at the apex, apical margins erose.

Common names — Amaa (Selogof); meraningga afok (Meyach); serrakh bekah, serrakh tetamos, tetamos (Maibrat); kiligata (Moi); benang (Hawodte); pèsèm; seockoe ma pote.

Distribution — Maluku Islands of Loloda Utara, Morotai, Halmahera, and Obi; northwestern Irian Jaya and adjacent Waigeo Islands, at 15–1200 m elevation (Fig. 1). This is the most widespread species, and it may be expected on other islands of the Maluku Islands (e.g., Bacan) and around Irian Jaya (e.g., Misool Island). Widespread in cultivation.

Notes — This species has long been in cultivation under the name Drymophloeus beguinii. Examination of the type specimens of D. beguinii, D. litigiosus, D. oninensis, and D. porrectus revealed only minor differences in leaf segment shape, from broadly flabellate in D. beguinii to narrowly cuneate in D. litigiosus. As leaf segment shape is highly variable in these understory palms and as that variation is continuous, I have chosen to recognize only one species. The name with priority is D. litigiosus, the meaning of which was not explained by Beccari.

Illustrations of this species, as *D. beguinii*, may be found in Moore (1953) and McCurrach (1960).

#### 4. Drymophloeus oliviformis (Giseke) Miq.

- Drymophloeus oliviformis (Giseke) Miq., Verh. Kon. Akad. Wet. Amsterdam, Natuurk. sect. II, 5 (1868) 24. Areca oliviformis Giseke, Prael. Ord. Nat. Pl. (1792) 79 ('olivaeformis'). Seaforthia blumei Kunth, Enum. Pl. 3 (1841) 192. Ptychosperma (Drymophloeus) rumphii Blume, Rumphia 2 (1843) 119, t. 83 & 156. Seaforthia oliviformis (Giseke) Mart., Hist. Nat. Palm. 3 (1849) 314. Saguaster oliviformis (Giseke) Kuntze, Revis. Gen. Pl. (1891) 734. Type: Saguaster minor, Rumphius, Herb. Amboin. 1 (1750) 67, t. 15.
- Drymophloeus ceramensis Miq., Palm. Archip. Ind. (1868) 5, 24. Type: Iter Moluccana, 1859– 1860, De Vriese & Teijsmann s.n. (holo L; photo BH).
- Drymophloeus bifidus Becc., Malesia 1 (1877) 44. Saguaster bifida (Becc.) Kuntze, Revis. Gen. Pl. (1891) 735. — Type: New Guinea, Mount Arfak at Putat, c. 300 m elev., Oct. 1872, Beccari 953 p.p. (holo FI-W; fragment K).
- Drymophloeus leprosus Zipp. ex Becc., Ann. Jard. Bot. Buitenzorg 2 (1885) 119. Saguaster leprosus (Zipp. ex Becc.) Kuntze, Revis. Gen. Pl. (1891) 735. Type: 'Ptychosperma rumphii' in Blume, Rumphia 2 (1836) t. 83 (excluding f. A). Suggested by 'Iriartea leprosa' Zipp. ex Macklot [nomen nudum, fide Henderson (1990)].

Solitary or weakly caespitose understory palm bearing 6 or 7 leaves. Stem 1–7 m tall, 2-7 cm diam.; stilt root cone 30 m tall. Leaf 86-250 cm long; petiole 21-61 cm long; sheath 15.5-70 cm long; 8-19 pairs of segments, middle segment 18-71 cm long, 3-24 cm wide, linear-lanceolate to broadly flabellate, borne 6-15 cm apart; terminal segments usually united to form a single flabellate segment, which may be slightly cleft. Inflorescence 18-30 cm long; prophyll 6-20 cm long, 1.3-2.7 cm wide, persistent; peduncular bract 8-28 cm long, 1.5-3.5 cm wide, dehiscing along the abaxial side, green and persistent; peduncle 7-26 cm long, 0.3-0.7 cm wide; rachillae 3-17, 75-405 mm long, 0.9-4.3 mm diam., with (4-)8-21 pistillate flowers per 5 cm. Staminate flower 5.2-10.2 mm long, 2.3-5.1 mm diam., greenish brown in bud; sepals reniform to semi-orbicular, 2-3.5 mm long, 4-4.9 mm wide; petals linear-elliptical to linear-ovate, greenish brown, 5.4-8 mm long, 2.6-4.4 mm wide; stamens 30-66, 4.2-5.1 mm long; filament 3.2-4.2 mm long; anther 1.9-3.5 mm long, 0.2-0.7 mm wide; pistillode 3.5-6 mm long, 1 mm diam., style 2-2.8 mm long. Pistillate flowers borne proximally or throughout the length of the rachillae, spirally arranged, sometimes distichously arranged distally, greenish brown, 3-5.7 mm long, 3-5.6 mm diam.; sepals

semi-orbicular, c. 3.5 mm long, c. 4.2 mm wide; petals semi-orbicular to reniform with cuspidate-valvate apices, c. 3.5 mm long, c. 3.5 mm wide; gynoecium conical, c. 4.3 mm long, c. 2.7 mm diam. *Fruit* red when ripe, fusiform to ovoid or obovoid, fleshy and juicy, 10.6–23.5 mm long, 5.5–11.9 mm diam.; exocarp smooth or finely rugose when dry; endocarp fusiform, inner wall caramel-colored, 8.6–17.9 mm long, 6.7–7.9 mm diam.; *seed* globose to ovoid, sometimes flattened at the base, brown, 4.7–11.3 mm long, 4.3–8.3 mm diam.; endosperm homogeneous. *Eophyll* elliptical, rarely shallowly notched at the apex, apical margins erose.

Common names — Menen, chibraka (Jougb); biasoi, sebu.

Distribution — Maluku Islands of Ambon, Buru, and Seram; Sula Islands; northwestern Irian Jaya, at 10–600 m elevation (Fig. 1). Widespread in cultivation.

Notes — The types of *D. bifidus*, *D. ceramensis*, *D. leprosus*, and *D. oliviformis* do not appear to differ in any significant and consistent way. That of *D. bifidus* has somewhat shorter and narrower leaf segments than the majority of the other specimens, but variation in segment size is continuous.

Seaforthia blumei was superfluous when published, as it was based on Ptychosperma (Drymophloeus) rumphii, which itself was superfluous, as it cited Areca oliviformis as a synonym. Both names therefore become synonyms of A. oliviformis and share its type. Kunth's description of S. blumei was based entirely on Blume's illustration, which appeared at least two years before the 1843 text.

Salomon (1887) placed *Pinanga bifida* Blume in synonymy with *Drymophloeus* bifidus Becc., erroneously supposing it to be a nomenclatural synonym. Blume's *Pinanga* is not based on the same type as *D. bifidus* and is not a species of *Drymophloeus*.

Drymophloeus oliviformis has a long history in cultivation. It is illustrated in a number of texts, including Moore (1953) and Langlois (1976).

#### 5. Drymophloeus pachycladus (Burret) H.E. Moore

Drymophloeus pachycladus (Burret) H.E. Moore, Principes 13 (1969) 76. — Rehderophoenix pachyclada Burret, Notizbl. Bot. Gart. Berlin-Dahlem 13 (1936) 87. — Type: Solomon Islands, San Cristobal, Kirakira, Brass 2720 [holo B (destroyed?); iso: BH, BISH, BO, BRI].

Solitary, emergent palm bearing 6–8 leaves. *Stem* 12–18 m tall, 8.9–35.6 cm diam.; stilt roots absent. *Leaf* 195–285 cm long; petiole c. 10 cm long; sheath 45–89 cm long; 27–39 pairs of segments, middle segment 29–72 cm long, 4.4–12.5 cm wide, linear-cuneate, borne 4.8–13.5 cm apart; terminal segments not united. *Inflorescence* 95–98 cm long; prophyll 43–56 cm long, 2.5–4.3 cm wide, caducous; peduncular bract 49–53 cm long, 2.3–2.5 cm wide, dehiscing along the abaxial side, caducous; peduncle 23–54.5 cm long, 0.9–2.3 cm wide; rachillae 5–12, 205–440 mm long, 3.5–9 mm diam., with 6–12 pistillate flowers per 5 cm. *Staminate flower* 9.1–16 mm long, 6.1–10.3 mm diam., green in bud; sepals reniform to semi-orbicular, 3.5–4.9 mm long, 5.5–8.4 mm wide; petals linear-elliptical to linear-ovate, greenish white, 7–14.6 mm long, 5.4–8.9 mm wide; stamens 174–320, 5.4–9.8 mm long; filament 4.3–8.2 mm long; anther 2.6–4.2 mm long, 0.4–0.7 mm wide; pistillode c. 2.7 mm long, c. 2.5 mm diam., style absent. *Pistillate flowers* borne throughout the length of the rachillae, spirally arranged proximally, distichously arranged distally, green, 9.1–10.1 mm long, 6.1–7.2 mm diam.; sepals semi-orbicular, 5.1–5.5 mm long, 6–7.1 mm

wide; petals semi-orbicular to reniform with cuspidate-valvate apices, 7.6-8.5 mm long, 6.1-7.5 mm wide; gynoecium conical, 6.9-7 mm long, 3.7-4 mm diam. *Fruit* red when ripe, fusiform to elongate elliptical, fleshy and juicy, 21-28 mm long, 9.8-11.8 mm diam.; exocarp smooth or finely rugose when dry, fiber ends visible; endocarp fusiform, bearing a single flattened ridge on one side, inner wall light brown; seed globose to ovoid, sometimes flattened at the base, brown, 13.3-17.2 mm long, 8.1-9.5 mm diam.; endosperm homogeneous. *Eophyll* bifid, apices erose.

Common names — Magi-magi, muggi-muggi (Wainoni); bulae-rondo (Kwara'ae).

Distribution — Solomon Islands (San Cristobal and Florida Islands), at 10-300 m elevation (Fig. 2). Occasionally cultivated in the Solomon Islands and in Florida, USA.

Notes — Although Burret's original description named *Brass 2730* as the type, the specimen *Brass 2720* is annotated as the type; '2730' is undoubtedly a typographical error.

This species (as 'D. pachyclades') was erroneously attributed to Irian Jaya and the Maluku Islands by Visser (n.d.).

This palm is uncommon in cultivation. It was illustrated by Dennis & McQueen (1989). Illustrations in Langlois (1976), identified as *Rehderophoenix pachyclada*, are more likely to be *D. subdistichus*.

#### 6. Drymophloeus subdistichus (H.E. Moore) H.E. Moore

Drymophloeus subdistichus (H.E. Moore) H.E. Moore, Principes 13 (1969) 76. — Rehderophoenix subdisticha H.E. Moore, Principes 10 (1966) 93. — Type: Solomon Is., Santa Isabel, Bogutu Peninsula, ridges behind Nangalo, near Tatamba, 20 Mar. 1964, Moore & Whitmore 9300 (= BSIP 2588) (holo BH; iso K, LAE).

Solitary, emergent palm bearing 7-15 leaves. Stem 5-25 m tall, 10.8-16.5(-30) cm diam.; stilt roots absent. Leaf 187-310 cm long; petiole 0-9.5 cm long; sheath 41-76 cm long; 23-39 pairs of segments, middle segment 45-65 cm long, 5.4-14 cm wide, linear-lanceolate, borne 5-11 cm apart; terminal segments not united. Inflorescence 50-91 cm long; prophyll 41-45 cm long, 5.3-8 cm wide, caducous; peduncular bract c. 50 cm long, dehiscing along the abaxial side, caducous; peduncle 12.5-19(-27) cm long, 1-1.7 cm wide; rachillae 15-40, 180-325 mm long, 2.3-4 mm diam., with 5-10 pistillate flowers per 5 cm. Staminate flower 9.4-12.5 mm long, 6.8-11 mm diam., green in bud; sepals reniform to semi-orbicular, 3.1-4.3 mm long, 5.2-5.9 mm wide; petals linear-elliptical to linear-ovate, greenish white, 8-11.3 mm long, 5.5-6.9 mm wide; stamens 135-219, 5.6-8.8 mm long; filament 5.6-7.7 mm long; anther 2.5-3.1 mm long, 0.5-0.7 mm wide; pistillode 1.5-4.8 mm long, c. 0.9 mm diam., style absent. Pistillate flowers borne throughout the length of the rachillae, spirally arranged proximally, distichously arranged distally, green, 4.1-8.5 mm long, 4-5.8 mm diam.; sepals semi-orbicular, 3.5–4.7 mm long, 3.5–8 mm wide; petals semi-orbicular to reniform with cuspidate-valvate apices, 4-5.9 mm long, 2.5-7.5 mm wide; gynoecium conical, 3-6.1 mm long, 1.2-2.3 mm diam. Fruit red when ripe, fusiform to elongate elliptical, fleshy and juicy, 16.9-24.6 mm long, 8.9-12.3 mm diam.; exocarp finely rugose when dry, fiber ends visible; endocarp fusiform, bearing a single flattened ridge on one side, weakly five-lobed at base, inner wall caramel-colored, 11.9–20.8 mm long, 6.9–11.8

mm diam.; *seed* globose to ovoid, sometimes flattened at the base, brown, 8.6–13.2 mm long, 7.1–9.4 mm diam.; endosperm homogeneous. *Eophyll* bifid, apices erose.

Common names — Fai basibasi, mamawa, sulu (Kwara'ae); boga.

Distribution — Solomon Islands (Guadalcanal, San Cristobal, and Santa Isabel), at 0–180 m elevation (Fig. 2). Occasionally cultivated in Florida, USA.

Notes — This palm is widespread on Guadalcanal, but populations are never large. It can be found in disturbed, secondary forests.

The species is illustrated in Figure 3b. It is also illustrated in Dennis & McQueen (1989) and in Langlois (1976), where it is misidentified as *Rehderophoenix pachyclada*.

#### 7. Drymophloeus whitmeeanus Becc.

Drymophloeus whitmeeanus Becc., Webbia 4 (1914) 261. — Solfia whitmeeana (Becc.) Burret, Feddes Repert. Spec. Nov. Regni Veg. 24 (1928) 281 ('withmeeana'). — Vitiphoenix whitmeeana (Becc.) Burret, Feddes Repert. Spec. Nov. Regni Veg. 24 (1928) 282. — Type: Samoa, Whitmee s. n. (holo K).

Solitary palm. *Leaf* segments 13; middle leaf segment c. 29 cm long, 5.4 cm wide, linear-cuneate. *Inflorescence* c. 80 cm long; peduncle 44 cm long, 1.3 cm wide; rachillae 15, 140 mm long and 2.1 mm diam., with 5 pistillate flowers per 5 cm. *Staminate flower* unknown. *Pistillate flower* unknown. *Fruit* probably red when ripe, fusiform to elongate elliptical, c. 37 mm long, 18.7 mm diam.; exocarp finely rugose when dry; endocarp fusiform, inner wall shiny brown; *seed* globose to ovoid, somewhat flattened at the base, brown, c. 16.9 mm long, 12.7 mm diam.; endosperm homogeneous. *Eophyll* unknown.

Common names — None recorded.

Distribution --- Western Samoa.

Note — This enigmatic species is known only from the type collection; my efforts to recollect this species in 1996 met with no success. The fruit and seed shape, as well as leaf segment shape, clearly suggest *Drymophloeus* and not any other Ptychospermatinae. The distribution of this palm, the easternmost species in the genus, is noteworthy. Additional collections of this Western Samoan palm, if it still exists, are greatly desired.

#### AMBIGUOUS NAMES

Coleospadix gracilis (Giseke) Burret, Feddes Repert. Spec. Nov. Regni Veg. 24 (1928) 285. — Areca olivaeformis var. gracilis Giseke, Prael. Ord. Nat. Pl. (1792) 80. — Type: Rumphius, Herb. Amboin. 1: 68. Sargile.

This name is based on a vague illustration in Rumphius. It cannot with certainty be applied to any known taxon (Moore, 1953).

Drymophloeus angustifolius (Blume) Mart., Hist. Nat. Palm. 3 (1849) 314. — Ptychosperma angustifolium Blume, Rumphia 2 (1843) 122 ('angustifolia'). — Saguaster angustifolius (Blume) Kuntze, Revis. Gen. Pl. (1891) 735. — Coleospadix angustifolius (Blume) Burret, Feddes Repert. Spec. Nov. Regni Veg. 24 (1928) 286. — Type: Rumphia 2: t. 156. Nomem ambiguum according to Essig (1978).

The type illustration in Rumphia is an ambiguous habit illustration providing no diagnostic characters.

Drymophloeus mooreanus Hort., Gard. Chron. ser. III, 33, 852 (1903) 266. — Type not designated.

This nomen ambiguum appeared in a description of new plants exhibited at a plant show in Europe. The complete description, "an erect palm with greyish-green leaves," is wholly inadequate to establish the identity of the palm.

Drymophloeus saxatilis (Burm.f. ex Giseke) Mart., Hist. Nat. Palm. 3 (1849) 314. —
Areca oryzaeformis var. saxatilis Burm.f. ex Giseke, Prael. Ord. Nat. Pl. (1792) 76. — Areca humilis Willd., Sp. Pl. 4, 1 (1797) 595. — Seaforthia saxatilis (Burm.f. ex Giseke) Mart., Hist. Nat. Palm. 3 (1838) 186. — Saguaster saxatilis (Burm.f. ex Giseke) Kuntze, Revis. Gen. Pl. (1891) 735. — Type: Pinanga saxatilis oryzaeformis, Rumphius, Herb. Amboin. 1: 42, t. 7.

The epithet *saxatilis* is said to have come from '*Areca saxatilis*', a name attributed to N.L. Burman [Fl. Indica (1768) 42] by Giseke and numerous subsequent authors, but which does not appear in Burman's work. Among the palms treated by Burman (on p. 241, not p. 42), nowhere is the name '*Areca saxatilis*' mentioned. The epithet was validated by Giseke's description.

The type illustration, t. 7 of Rumphius, shows a rhizomatous palm from Sulawesi and Ambon with deltoid and erose leaf segments. The inflorescence, bearing mostly pistillate flowers proximally, is shown with a long peduncle that is strangely swollen in the middle. This growth habit is unknown in *Drymophloeus*, and the swelling of the peduncle may be pathological in origin. The name may apply to a species of *Areca* or *Pinanga*.

## EXCLUDED NAMES

- Drymophloeus ambiguus Becc., Malesia 1 (1877) 42, 98. Saguaster ambiguus (Becc.) Kuntze, Revis. Gen. Pl. (1891) 735 = Ptychosperma ambiguum (Becc.) Becc.
- Drymophloeus appendiculatus (Blume) Miq., Palm. Archip. Ind. (1868) 24. Saguaster appendiculata (Miq. ex Becc.) Kuntze, Revis. Gen. Pl. (1891) 734; nomen illeg. et superfl.

According to Beccari [Ann. Jard. Bot. Buitenzorg 2 (1885) 122], this name is based on *Ptychosperma appendiculatum* Blume, Rumphia 2 (1886) 119, 122. t. 84 & 119 (as 'appendiculata'), although Miquel gave no explicit indication that he had Blume's species in mind. Blume's *P. appendiculata* is itself an illegitimate and superfluous name, in that Blume cited as synonyms two legitimate names of Giseke (*Areca vaginata* Giseke and *A. olivaeformis* var. gracilis Giseke). Blume's type illustration (t. 84) shows *D. oliviformis* with a slightly split apex to the leaf and a stout inflorescence; hence, the name *D. appendiculatus* has been misapplied to *D. oliviformis* even though it is illegitimate.

Drymophloeus communis Miq., Palm. Archip. Ind. (1868) 24; nomen nudum.

Drymophloeus divaricatus (Brongn.) Benth. & Hook. ex Becc., Ann. Jard. Bot. Buitenzorg 2 (1885) 168 = Actinokentia divaricata (Brongn.) Dammer.

- Drymophloeus filiferus (H. Wendl.) Scheff., Ann. Jard. Bot. Buitenzorg 1 (1876) 137 = Veitchia filifera (H. Wendl.) H.E. Moore.
- Drymophloeus jaculatoria Mart., Hist. Nat. Palm. 3 (1838) 186 & (1849) 314; nomen illeg. et superfl.

This name is both illegitimate and superfluous because Martius cited Areca vaginata Giseke and A. olivaeformis var. gracilis Giseke as synonyms.

- Drymophloeus kirstenianus Sander ex Burret, Feddes Repert. 24 (1928) 263 = Ptychosperma kerstenianum (Hort. ex Sander) Burret.
- Drymophloeus mambare F.M. Bailey, Queensland Agric. J. 3 (1898) 202 = Ptychosperma mambare (F.M. Bailey) Becc.
- Drymophloeus minutus Rech., Denkschr. Akad. Wien 85 (1910) 237 = Balaka minuta (Rech.) Burret.
- Drymophloeus montanus K. Schum. & Lauterb., Fl. Schutzgeb. Südsee (1901) 207 = Ptychosperma caryotoides Ridl.
- Drymophloeus normanbyus (F. Muell.) Benth. & Hook. ex Becc., Ann. Jard. Bot. Buitenzorg 2 (1885) 168. Saguaster normanbyi (F. Muell.) Kuntze, Revis. Gen. Pl. (1891) 735 = Normanbya normanbyi (W. Hill) L.H. Bailey.
- Drymophloeus ? paradoxus Scheff., Ann. Jard. Bot. Buitenzorg 1 (1876) 53, 121 = Ptychococcus paradoxus (Scheff.) Becc.
- Drymophloeus pauciflorus (H. Wendl.) Becc. ex Martelli, Atti Soc. Tosc. Sci. Nat. Mem. 44 (1934) 151. Saguaster pauciflorus (H. Wendl.) Kuntze, Revis. Gen. Pl. (1891) 735 = Balaka pauciflora (H. Wendl.) H.E. Moore.
- Drymophloeus propinquus Becc., Malesia 1 (1877) 43.—Saguaster propinquus (Becc.) Kuntze, Revis. Gen. Pl. (1891) 735 = Ptychospermum propinquum (Becc.) Becc.
- Drymophloeus propinquus var. keiensis Becc., Malesia 1 (1877) 43 = Ptychospermum propinquum (Becc.) Becc.
- Drymophloeus puniceus Becc., Malesia 1 (1877) 47. Saguaster punicea (Becc.) Kuntze, Revis. Gen. Pl. (1891) 735 = Pinanga punicea (Zipp. ex Blume) Merr.
- Drymophloeus reineckii Warb. in F. Reinecke, Bot. Jahrb. Syst. 25 (1898) 590. Lectotype, designated here: Samoa, Upolu, Letogo Ridge, March 1894, *Reinecke* 205 (lecto BO) = Balaka tahitensis (H. Wendl.) Becc.

Warburg designated two syntypes, *Reinecke 205* and *Reinecke 631*. As noted by Whistler (1992), the two syntypes are referable to two different species of *Balaka*, *B. tahitensis* (H. Wendl.) Becc. and *B. brachychlamys* Burret. The choice of lectotype, the more complete of the two syntype specimens, places *D. reineckii* in synonymy of *Balaka tahitensis*.

- Drymophloeus rumphianus Mart., Hist. Nat. Palm. 3 (1849) 314 = Pinanga punicea (Zipp. ex Blume) Merr.
- Drymophloeus samoensis (Rech.) Becc. ex Martelli, Nuov. Giorn. Bot. Ital. 42 (1935) 44 = Sofia samoensis Rech.
- Drymophloeus schumannii (Becc.) Warb. ex K. Schum. & Lauterb., Fl. Schutzgeb. Südsee (1901) 207 = Brassiophoenix schumannii (Becc.) Essig.
- Drymophloeus seemannii (H. Wendl. ex Seem.) Becc. ex Martelli, Atti Soc. Tosc. Sci. Nat. Mem. 44 (1934) 151.—Saguaster seemannii (H. Wendl. ex Seem.) Kuntze, Revis. Gen. Pl. (1891) 735 = Balaka seemannii (H. Wendl.) Becc.
- Drymophloeus singaporensis (Becc.) Hook., Kew Rep. 1884 (1882) 55 = Rhopalablaste singaporensis (Becc.) H.E. Moore.
- Drymophloeus vestiarius Miq., Palm. Archip. Ind. (1868) 24; nomen nudum, but possibly = Areca vestiaria Giseke.
- Drymophloeus zippelii Hassk., Hoeven & De Vriese, Tijdschr. Natuurl. Gesch. Physiol. 9 (1842) 170 = Caryota mitis Lour.
- Saguaster capitis-yorkis (H. Wendl. & Drude) Kuntze, Revis. Gen. Pl. (1891) 735 = Ptychosperma elegans (R. Br.) Blume.
- Saguaster drudei (H. Wendl.) Kuntze, Revis. Gen. Pl. (1891) 735 = Archontophoenix alexandrae (F. Muell.) H. Wendl. & Drude.
- Saguaster elegans (R. Br.) Kuntze, Revis. Gen. Pl. (1891) 735 = Ptychosperma elegans (R. Br.) Blume.
- Saguaster gracilis (Labill.) Kuntze, Revis. Gen. Pl. (1891) 735 = Ptychosperma gracile Labill.
- Saguaster macarthurii (H. Wendl. ex Veitch) Kuntze, Revis. Gen. Pl. (1891) 735 = Ptychosperma macarthurii (H. Wendl. ex Veitch) H. Wendl. ex Hook.f.
- Saguaster perbrevis (H. Wendl.) Kuntze, Revis. Gen. Pl. (1891) 735 = Balaka seemannii (H. Wendl.) Becc.
- Saguaster pickeringii (H. Wendl.) Kuntze, Revis. Gen. Pl. (1891) 735 = Veitchia pickeringii (H. Wendl.) H.E. Moore.
- Saguaster tahitensis (H. Wendl.) Kuntze, Revis. Gen. Pl. (1891) 735 = Balaka tahitensis (H. Wendl.) Becc.
- Saguaster vitiensis (H. Wendl. ex Seem.) Kuntze, Revis. Gen. Pl. (1891) 735 = Veitchia vitiensis (H. Wendl. ex Seem.) H.E. Moore.

#### ACKNOWLEDGEMENTS

Many individuals and institutions contributed, either materially or emotionally, to the success of this work, and I am grateful to them all. I especially thank my companions in the field: the late G. Dennis, J. Dransfield, S. Dransfield, A. Prihardyanto Keim, R. Maturbongs, W. McClatchey, C. Schuster, M. Qusa Sirikolo, T. Tipamaa, P. Tofu, A. Whistler, and the many local people who smoothed the way for me. For their stimulating discussion, thoughtful comments, and generous insights, I thank G. Dennis, J. Dransfield, F. Essig, M. Ferrero, J. Fisher, W. McClatchey, N. Uhl, and the anonymous reviewers of the manuscript. I thank the curators of the cited herbaria for access to the specimens in their care, and I am grateful for all the 'ground support' given by B. Baker, S. Barrow, I. Haerida, S. Kennedy, H. Sanderson, and the staff of Fairchild Tropical Garden.

Financial support came from Fairchild Tropical Garden through its FEMA Tree Replacement funds, the South Florida Chapter of the International Palm Society, and the Broward County [Florida] Palm and Cycad Society. Thank you all!

#### REFERENCES

- Audley-Charles, M.G. 1981. Geological history of the region of Wallace's Line. In: T.C. Whitmore (ed.), Wallace's Line and plate tectonics: 24–35. Oxford University Press, Oxford.
- Beccari, O. 1877a. Le specie di palme raccolte alla Nuova Guinea da O. Beccari e deal medesimo adesso descritte, con note sulle specie dei paesi circonvicini. Malesia 1: 8-96.
- Beccari, O. 1877b. Nouve osservazioni sulle palme della Nuova Guinea. Malesia 1: 97-102.
- Beccari, O. 1885. Reliquiae Schefferianae. Illustrazione di alcune palme viventi nel Giardino Botanico di Buitenzorg. Ann. Jard. Bot. Buitenzorg 2: 77–171.
- Beccari, O. & R.E.G. Pichi-Sermolli. 1955. Subfamiliae arecoidearum palmae gerontogeae: tribuum et generum conspectus. Webbia 11: 1–187.
- Burret, M. 1936. Neue Palmen aus Neuguinea III. Zugleich Palmen von den Salomo-Inseln. Notizbl. Bot. Gart. Berlin-Dahlem 13: 65–101.
- Dennis, G. & D. McQueen. 1989. Palms in the Solomon Islands. In: J.L. Dowe (ed.), Palms of the Solomon Islands: 8-45. Palm & Cycad Societies of Australia, Milton, Qld.
- Essig, F.B. 1978. A revision of the genus Ptychosperma Labill. (Arecaceae). Allertonia 1: 415-478.
- Essig, F.B. 1987. A new species of Ptychosperma (Palmae) from New Britain. Principes 31: 110-115.
- Essig, F.B. 1995. A checklist and analysis of the palms of the Bismarck Archipelago. Principes 39: 123-129.
- Fairchild, D. 1942. More plants from the Fairchild Garden expedition to the Philippines and Netherlands India. Fairchild Trop. Gard. Occas. Paper 10: 1–10.
- Farris, J.S. 1988. Hennig86. Port Jefferson Station, New York.
- Hay, A.J.M. 1984. Palmae. In: R.J. Johns & A.J.M. Hay (eds.), A guide to the Monocotyledons of Papua New Guinea: 195-318. Papua New Guinea University of Technology, Lae.
- Henderson, A. 1990. Arecaceae. Part 1. Introduction and the Iriarteinae. Flora Neotropica 53: 1-101.
- Langlois, A.C. 1976. Supplement to Palms of the World. University Presses of Florida, Gainesville.
- Martelli, U. 1935. La sinonima delle palmae gerontogee dela tribú delle Arecacee. Nuovo Giorn. Bot. Italiano 42: 17–88.
- McCurrach, J.C. 1960. Palms of the world. Harper & Bros., New York.
- Moore Jr., H.E. 1953. Exotic palms of the western world. Gentes Herb. 8: 295-315.
- Moore Jr., H.E. 1958. What's in a name? Principes 2: 141, 142.
- Moore Jr., H.E. 1969. New palms from the Pacific, II. Principes 13: 67-76.
- Read, R.W. 1966. New chromosome counts in the Palmae. Principes 10: 55-61.
- Ridgeway, J. 1987. Neogene displacements in the Solomon Islands arc. Tectonophysics 133: 81– 93.

- Salomon, C. 1887. Die Palmen nebst ihren Gattungen und Arten für Gewächshaus- und Zimmer-Kultur. Verlag von Paul Parey, Berlin.
- Scheffer, R.H.C.C. 1876. Sur quelques palmiers du groupe des Arécinées [part 2]. Ann. Jard. Bot. Buitenzorg 1: 103-164, pl. 1-30.
- Thanikaimoni, G. 1971. Les palmiers: Palynologie et systématique. Inst. Franç. Pondichéry Trav. Sect. Sci. Tech. 11: 1–286, pls. 1–22.
- Tomlinson, P.B. 1990. The structural biology of palms. Oxford University Press, Oxford.
- Uhl, N.W. & J. Dransfield. 1987. Genera palmarum. A classification of palms, based on the works of Harold E. Moore, Jr. Allen Press, Lawrence, Kansas.
- Visser, M.B.H. n.d. 100 Macam palem di Indonesia. [Published without imprint.]
- Watson, W. 1891. New or little-known plants: Drymophloeus olivaeformis. Gard. & For. 4, 177: 330, 331.
- Whistler, W.A. 1992. The palms of Samoa. Mooreana 2, 3: 24-29.
- Zona, S. 1999. New perspectives on generic limits and relationships in the Ptychospermatineae (Arecaceae: Arecoideae). In: A. Henderson & F. Borchsenius (eds.), Evolution, variation, and classification of Palms. Mem. New York Bot. Gard. (in press).

#### **IDENTIFICATION LIST**

4. oliviformis
5. pachycladus
6. subdistichus
7. whitmeeanus

Anonymous 68 (FI): 4 — Anonymous [cult. Bogor] (BO): 3 — Anonymous [cult. Bogor] (FI): 4. Baker 89024-2: 4 — Beccari 59: 3; 511: 3; 511bis: 3; 616: 4; 953 p.p.: 4 — Beguin 1930: 3; 2347: 3 — Bloembergen 4467: 4; 4683: 4 — Brass 2720: 5.

- Coons 1683: 5 Corner RSS 7: 5 Curran FTG 402: 3.
- Davis et al. 723: 3 De Vogel 4038: 3 Dennis RSS 53: 2; BSIP 4445: 6.
- Ellen 77: 4 Essig & Katik LAE 64061: 1 Eyma 2119: 4; 2185: 4.
- Gafui et al. BSIP 12605: 6.
- Henderson 292: 6 Hill 2631: 3 Hodel & Hodel 1145: 1.
- Kornassi 1553: 4 Kostermans et al. 1117: 3.
- Langlois FTG 331: 3.
- Millar 40558: 1 Mogea & Ismail 5158: 4; 5223: 4 Moll BW 9762: 3 Moore 6034: 3; 6142: 3 Moore & Langlois 5863: 4 Moore & Whitmore 9300 [= BSIP 2588]: 6.
- Pleyte 351: 3 Powell BSIP 19361: 5.
- Read 1395: 3 Robinson 21: 4; 22: 4 Rutten 1794: 4; 2190: 4.
- Schoute 105: 4 --- Stone 2273: 6.
- Teijsmann 7820: 4 --- Toxopeus 320: 4.
- Van Balgooy 4714: 4; 4906: 4 Van Royen 3160: 4; 3454: 3; 5489: 3.
- Whitmore BSIP 3808: 6.
- Zona 486: 5; 666: 5; 708: 6; 764: 4; 766: 5; 767: 6; 769: 5 Zona & Hausman 605: 4; 641: 6 Zona et al. 646: 6; 653: 6; 659: 6; 660: 6; 664: 5; 668: 4; 668b: 3; 680: 3; 682: 3; 684: 4; 685: 4; 686: 3; 687: 4; 696: 3.