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THE NEW GUINEA SPECIES OF PANDANUS SECTION MAYSOPS ST. JOHN (PANDANACEAE)

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SUMMARY

Species of *Pandanus* belonging to section *Maysops* St. John [this section is presently classified under subgenus *Lophostigma* (Brongn.) Stone], about 16 in all, occur in New Guinea, the adjacent Moluccas, the Bismarck Archipelago, the Solomon Islands, and Northern Queensland, Australia. The majority (11) of the species are found in, and mostly limited to, New Guinea. Here these 11 species are reviewed, a key for identification is presented, and information on synonymous names, distribution, and certain critical aspects of morphology is included. In an appendix, the remaining species assigned to section *Maysops* are briefly listed. There are probably a few undescribed species.

INTRODUCTION

Pandanus section *Maysops* St. John (1960) groups those species sharing a number of characters of the fruit, especially the locular number (1), form of the stigma, and of the cephalium. Later it has become clear that this section is very homogeneous also in features of the staminate flowers and inflorescences. Huynh (1974, 1976) then demonstrated that the suite of micromorphological and anatomical characters of the leaves formed further strong support for the naturalness of the section. Moreover, as the full geographical distribution became clear this too can be seen as further strengthening the taxonomic concept which rested, at first, entirely on a few characters of the pistillate organs.

Section Maysops: diagnosis and relationships

Species belonging to section *Maysops* can now be defined as those which share the following diagnostic features: — *Pistillate:* solitary, usually ovoid-ellipsoid cephalia, closely sheathed in several series of persistent bracts, composed of numerous free simple carpels each of which develops into a drupe; the pileus (drupe apex) low, not separately caducous, with a small, slightly excentric stigmatic apparatus usually in the form of a small hardened turret nearer the adaxial rim, the stigma often slightly overtopped by a so-called 'stylar visor' (the Latin term used for this will be *petasus*, meaning a broad-brimmed hat) which is more or less clearly, though minutely toothed (usually with 2–4 dentations); the stigmatic surface oblique or vertical, on the adaxial surface, small and usually wider than long; pericarp tissue containing some oil or fat; small bony endocarp with a single seed; and a mesocarp that contains in the upper part (uniting the ovular and pilear zones) several thick, fusiform, distally incurved fibers. — *Staminate:* inflorescence of several thick spikes, each formed of numerous crowded staminate flowers, these typically of about 6–12 stamens, their filaments basally connate, sometimes almost completely united in a staminal tube, the free upper parts clearly bulbous (often brightly colored) and very abruptly differentiated from the free *pendiculus* (short basal prolongation of the connective; the term was introduced by Stone, 1990), the anther oblong, its apex apiculate by a short or long extension of the connective, the tip of which is acute, entire, not tufted, but dotted unilaterally with crystalliferous cells; pollen sometimes distinctly oily, the grains sometimes adherent in irregular groups in the 'pollenkitt'. — *Vegetative:* erect trees (or shrubby) with rigid proproots; leaves with the apical ventral pleats prickly.

Section Maysops is closely related to a few other endemic New Guinea sections, especially to section Metamaysops Stone (1974) and section Perrya Stone (1974). Another relationship, still incompletely understood, is to Pandanus pendulinus Martelli, originally thought to belong to section Acrostigma but as shown by Stone & Huynh (1983) definitely a species in subgenus Lophostigma and possibly representing an as yet undescribed section allied to section Maysops.

Historical perspective

The earliest species of section *Maysops* described was *Pandanus amboinensis* Warb., but the first name applied to it was *Pandanus silvestris* Rumphius, published in 1743; though introduced by Kunth (in 1841) and Miquel (in 1855) into the post-Linnaean nomenclature as *P. silvestris*, that name had been preempted by *P. sylvestris* Bory (1804), hence Warburg's renaming of the species. Rumphius' plant came of course from Amboina; and this species seems still to be the only one of the section occurring in the Moluccas, although it is here considered to occur in New Guinea as well.

The next species to be described, *Pandanus beccarii* Solms, dates from 1883; this was followed by *P. krauelianus* K. Schum. in 1889. Martelli added *P. flabellistigma* in 1905 (here reduced to *P. krauelianus*); Rendle described *P. tabbersianus* in 1917. In 1929, Martelli described *P. kivi* (regarded here as a synonym of *P. tabbersianus*). Finally, after studying material collected by L.J. Brass during the Archbold Expeditions in New Guinea, Merrill & Perry (1939) added several species, of which *P. xanthocarpus*, *P. cernuifolius*, and *P. microdontus* are retained. The remaining species have all been discovered or described since 1950, including the sole species known from Australia (*P. zea* St. John) and the four species occurring in the Bismarck Archipelago and the Solomon Islands (*P. flavicarpus* Stone, *P. roseus* Stone, *P. rubellus* Stone, and *P. spodiophyllus* Stone). Full accounts of these species can be found in St. John (1960) and Stone (1972). The most recently described species is *P. kosteri* (Stone, 1987).

Taxonomy

The identification of species has proved considerably more difficult than the diagnosis of the section *Maysops*. St. John typified the section with his then new species P. zea; and there has not been any real difficulty encountered in assigning species to the section, as the type species was represented by full modern collections of both sexes. However, as is usual in this genus, most species have been based on pistillate materials, often rather poorly collected or preserved. St. John (1973) and Stone (1965, 1974, 1987) added further species. In addition, St. John had over the course of several years annotated specimens (from various herbaria) with unpublished names, some of which have appeared as *nomina nuda* in papers either by St. John himself or by others, in some cases with different names for duplicata of the same number in different herbaria, which can lead of course to confusion.

It has become apparent that undue reliance on such data as drupe length and leaf measurements based on one or two collections may suggest taxonomic differences which are only artifacts of collecting – selection of leaves by the collector, age of the fruit, or age of the plant. Other differences may be real but based on small variations in populations of which there is seldom sufficient field knowledge to reveal the limits of variability. Moreover, earlier descriptions tended to lack sufficient scope and/or precision. Identification of staminate material, not to mention sterile collections, proved difficult when most or all diagnostic features were those of the fruit or pistillate structures. While shortcomings of earlier collections cannot be remedied, it is hoped that new collections will be based on a knowledge of what needs to be obtained (Stone, 1983) and how they may be properly preserved. Collectors are strongly urged to supplement specimens with notes and photographs or drawings which can help to overcome the problems of representing these bulky plants in ways that permit a greater insight into their habits of growth, habitat characteristics and associated plants, developmental stage, variability, and ephemeral or subtle features.

The present revision is based on personal field work in Papua New Guinea and in the Bismarck Archipelago and the Solomon Islands, on examination of all type specimens and most other collections represented in most major herbaria. It is a conservative treatment and reduces several published names to synonymy. On the other hand, there is a fairly strong likelihood that further discoveries will be made in areas as yet incompletely collected, so that the total number of species accepted here is still a provisional one.

The center of evolution for section Maysops is clearly within New Guinea and the eastern Melanesian islands (New Britain, New Ireland, and the Solomon Islands). Most of the species are comprised of small to medium arborescent plants, but one species appears almost as a dwarf (P. kosteri); the larger ones may reach a height of about 16 m. The trunk may be simple, but usually at length branches, sometimes somewhat abundantly to form a spreading crown. Proproots, in some species of considerable length and diameter and forming stilts, are generated from the trunk (and rarely from some large branches). The fruit heads are invariably solitary, ovoidellipsoid in form and mostly 15-40 cm long, closely sheathed by the persistent bracts. These bracts, at anthesis variously colored, wither to a dull pale brown. The head consists of numerous drupes, which ripen basipetally, those at the tip of the head falling first; the pericarp is typically yellow, pink, or red, the pileus sometimes of a contrasting tint, and the tissue is thin fleshy, slightly oily. The pileus is persistent, but shrinks on drying. The pileus may be convex or have a peripheral rim (accentuated in dry specimens); there is a submarginal turret of hard glossy tissue on which the stigma is positioned. The oily pericarp is sometimes used as a food substitute for the 'marita' (Pandanus conoideus Lamk.).

The staminate inflorescence usually hangs below the leafy crown; as the trees are themselves understorey denizens in rain forest, the flowers are protected above but accessible from below. In the few cases where fresh staminate inflorescences were observed, the pollen exhibited a noticeable pollenkitt, such that the pollen on release may fall in irregular groups of grains; the oil is slightly yellowish. The staminate flowers of all species so far known have a common basic structure, with the stamens connate into a basal tube, with the filaments, if at all free distally, bulbous and colored. The anther is attached by a pendiculus (basal prolongation of the connective), a structure homologous (presumably) with the anther apiculus, but distinct from that in regard to the occurrence of crystalliferous cells, and sharply differentiated from the filament (Stone, 1990). There are often 6 stamens per flower, but the number varies and as many as 12-15 may occur. The relative rigidity of the tube and the filaments, and the flexibility of the slender pendiculi, permits the anthers to move or vibrate and (perhaps) facilitates the shedding of pollen from the anther sacs. These characters in conjunction with the pollen as described above appear to form a set of correlated characters which probably plays a determinative role in the pollination biology of these species. Anthesis (as noted in LAE 53802) occurred toward evening, perhaps suggesting bat-pollination.

Foliar micromorphology and anatomy in relation to taxonomy

The pioneering work of Tomlinson (1965) and Kam (1971), carried to a wider range of species and to a greater depth of detail by Huynh (1974, 1976), demonstrated that microscopic characters, particularly those of the foliar epidermis and some features of the internal anatomy, were significant taxonomically. In his survey of a selection of species representing most of the subgenera and sections of *Pandanus*, Huynh (1976) summarized the foliar micromorphological characters of section *Maysops* as follows:

Abaxial stomatic apparatus complex, varying from class VI to class VII; non-stomatic adaxial epidermal cells usually with obscure lateral pits; frequent presence of fibers in the medullary tissue; adaxial hypodermis of 2–4 layers of cells; adaxial spongy tissue of 1 layer, poor or lacking in fibers; adaxial stomata about 29 μ m; abaxial stomata about 20 μ m; abaxial zonation usually clear; adaxial and abaxial chlorenchyma usually discontinuous; hypodermal crystals abundant.

While section *Maysops* can be considered a more or less homogeneous group in regard to its abaxial stomatal characters, the microscopic morphology in general shows some variation that deserves further consideration. This variation particularly involves the degree of complexity of the stomatal apparatus, and the medullary tissue of the leaf. Huynh (l.c.) suggests that *P. beccarii* (and two synonymous species), with stomatal apparatus of class VII, lack of fibers in the medullary tissue, and abaxial epidermis thick (27 μ m), could form a possible subgroup, in contrast with the more frequent suite of characters in other species of the section (stomatal apparatus of class VI; presence of fibers in the medullary tissue, and thinner abaxial epidermis). There appears no correlation of such groups at this stage with gross morphological characters.

SYSTEMATIC TREATMENT

Pandanus section Maysops

Pandanus section Maysops St. John, Pacif. Sci. 14 (1960) 227; Stone, Bot. Jahrb. 94 (1974) 497; Huynh, Bot. Jahrb. 97 (1976) 91. — Type species: Pandanus zea St. John (1960).

Arborescent pandans, stems erect, branched, with basal proproots. Leaves with apical ventral pleats prickly. Pistillate cephalium of free carpels ripening as simple drupes. Pileus persistent. Stigma small, borne on the adaxial margin of the pileus or on a turret within the pilear rim, erect, wider than long, overtopped by a toothed stylar visor. Outer fibers of apical mesocarp fusiform. Staminate spikes compound, pendulous. Stamens basally connate, partly or almost completely, tubular, formed usually of about 6-12 stamens, the filaments colored, clavoid or bulbous and at apex abruptly differentiated from the white, thread-like, flexible (when fresh) pendiculus; anther oblong, apiculate, the apiculus entire, crystalliferous. Pollen grains with a light oily pollenkitt. Fruit sheathed by persistent bracts; bract margin prickly toward base and distally, with a distinct median interruption (there entire).

Distribution – Moluccas (Amboina), New Guinea, N Queensland, Bismarck Archipelago, Solomon Islands; about 16 species.

KEY TO THE SPECIES

1	
	broadly acute. Leaf margins with small equal prickles 1. P. kosteri
	cm. Drupes red, $15 \times 4-5$ mm. Leaf midrib proximally unarmed. Apex of blade
1a.	Small shrubs to c. 1.5 m tall. Cephalium small, oblong-ellipsoid, c. 6.5×3.5

5a.	Drupes pink, 20×4 mm, the pileus slightly concave. Cephalium c. 25 cm long,
	8.5 cm wide. Leaves c. 275-300 cm long, 6.8-8.5 cm wide
	3. P. microdontus
b.	Drupes red, $20-25(-27) \times 4-6$ mm, the pileus with convex turret. Cephalium
	c. 32-45 cm long, (7-)11-14 cm wide. Leaves usually 300-400 cm long,
	7–11.2 cm wide 4. P. beccarii
6a.	Ripe fruits yellow, the pericarp yellow throughout (not orange or red, not bi-
	colored). Stylar visor usually 3-more-toothed (rarely only 2-toothed), usually
	evidently excentric. Drupe apex slightly concave
b.	Ripe fruit purplish to red, vermilion, orange, or pink. Stylar visor 1- or 2-tooth-
	ed (rarely more), sometimes deltoid, often situated on a subcentral rounded tur-
	ret 10
-	

7a. Drupes 12–13 mm long, 4–5 mm wide. Cephalium 28–41 cm long. Style flattened, visor 2-toothed. Leaves large, 200–400 cm long, 7–12 cm wide

6. P. croceus

- - b. Drupes longer, 17-25 mm long. Cephalium 19-45 cm long, ovoid subcylindric. Leaves 5-10 cm wide 11

1. Pandanus kosteri B.C. Stone

Pandanus kosteri B.C. Stone, Blumea 32 (1987) 435, f. 5. — Type: Koster BW 6852, West Irian. Pandanus cernuus St. John, nom. ined. in herb.; ex Huynh, Bot. Jahrb. 97 (1976) 92, nom. nud.

A semi-dwarf pandan to 1.7 m tall, stem erect, distally c. 1 cm diam. Leaves 68-100 cm long, 2.5-3.7 cm wide, sheathing base 2.5 cm long, with narrow subauricular margin; blade linear, broadly acute acuminate, at base somewhat narrowed. Upper surface smooth, lower surface rather smooth with rather indistinct veins, slightly paler. Longitudinal veins about 48-68 per leaf. Margins near base with slender spreading prickles 1-2 mm long, mostly 1-5 mm apart; near middle, the prickles antrorsely curved, subappressed, 0.3-0.7 mm long, 1-7 mm apart; near apex, the

prickles 0.2–0.66 mm long, 0.9–2.5 mm apart. Midrib near base with few retrorse prickles to 2 mm long, or these usually nub-like or lacking entirely; near the middle, the midrib carinate, entire; near apex (distal fourth or fifth) with small antrorse prickles 0.2-0.4 mm long, 1-5(-15) mm apart, except at extreme tip where they are spaced as on the adjacent margin. Apical ventral pleats with a few antrorse prickles along distal third, 0.3-0.5 mm long, 3-15 mm apart, sometimes reduplicate, lacking on extreme tip, unevenly distributed. Inflorescences terminal, pendent, bracteate. Pistillate cephalium on peduncle c, 12 cm long, 6 mm thick. Bracts ovate navicular acute, 7-13 cm long, c. 6 cm wide, distally prickly on margins, keel and apical-ventral pleats, base slightly expanded outward. Cephalium small solitary, short oblong ellipsoid, 65 mm long, 35 mm wide, composed of many small red drupes 15 mm long, 4-5 mm wide, cuneiform, truncate; pileus 2-3 mm high, 5-6-angled, centrally concave and with a central turret bearing distally a depressed, briefly extended stylar visor 0.75 mm long, 1 mm wide, 2-toothed, stigma transverse, reniform, 1-1.5 mm wide, beneath the visor or slightly exposed or reflexed. Upper mesocarp fibrous, the claviform or fusiform fibers incurved, lower mesocarp fleshy fibrous. Endocarp c. 6 mm long, ellipsoid, subcentral, the walls 0.5-0.7 mm thick. Staminate inflorescence a bracteate spadix 50-55 cm long, on a slender peduncle c. 5 mm wide; lower bracts foliaceous; intermediate bracts green-tipped; upper bracts navicular concave, c. 30 cm long, 5.5 cm wide, the internodes 3-5 cm long. Fertile bracts 5 or 7, c. 17×6 to 6×1 cm or smaller. Spikes oblong, 3-8 cm long, 9-13 mm wide, composed of numerous phalanges, these 5-9-staminate; staminal tube smooth, to 3 mm long, 1.5-1.8 mm wide, somewhat compressed bilaterally, dotted with raphidophorous cells, the interior hollow obconic; filament apex very short, obtuse, abruptly narrowed into the subterete, flexible, slender pendiculus c. 0.2 mm long; anther oblong. 3 mm long, rounded at base, acuminate at apex and apiculate, thecae c. 2 mm long, apiculus c. 1 mm long, dotted with raphidophorous cells.

Distribution - New Guinea, endemic, known from two collections from West Irian.

Habitat – In primary forest with oaks, 950–1300 m alt., clay soil. Stam. fl. 27 Feb.; fr. 17 Feb.

Note – The small stature, red bracts, and red fruits distinguish this species. The leaf medullary tissue includes abundant fiber bundles. Abaxial stomata are intermediate in complexity between class VI and class VII. The chlorenchymata are continuous.

INDONESIA — West Irian: Kebar, Sanopi, 1300 m, 17 Feb. 1958, Koster BW 6852 (L, holo). Wondiwoi Mts, Wandammen Peninsula, 950 m, 27 Feb. 1962, Koster BW 13646 (L).

2. Pandanus xanthocarpus Merr. & Perry

Pandanus xanthocarpus Merr. & Perry, J. Arnold Arbor. 20 (1939) 179, pl. 1, f. 17; St. John, Pacif. Sci. 14 (1960) 227; Stone, Bot. Jahrb. 94 (1974) 497. — Type: Brass 8487, New Guinea.

Pandanus maneauensis St. John, nom. ined. in herb.; ex Huynh, Bot. Jahrb. 97 (1976) 93, nom. nud.

Tree 6–7 m tall, trunk branched above, at base with crowded proproots to 1 m long. Leaves 150–170 cm long, 7.5–8 cm wide, flexible, dilated at base, gradually acuminate distally, glaucous beneath; longitudinal veins more evident distally, obscure proximally, distal portion of apical ventral pleats sporadically and subremotely prickly. Midrib above channelled, beneath carinate, in distal part rather remotely prickly. Margins near base with closely set spreading prickles, sharp subulate, those along more distal part antrorse, not spreading. *Inflorescence* unknown. *Immature infructescence* a solitary, pendent, oblong ovoid cephalium, sheathed in crowded bracts longer than the fruit head, c. 22 cm long, 11 cm diam., composed of numerous simple, elongate, pale yellow drupes, these each c. 30–32 mm long, 3–4 mm wide, linear, prismatic, 5–6-angled, slightly narrowed toward base; pileus 3–3.5 mm high, obtusely angled, apex concave but with central pyramidal turret 0.5–0.7 mm high, its vertex flat and bearing the extremely short slightly 2-lobed or -toothed stylar visor and bilobate-dentiform stigma. Upper mesocarp pithy fibrous. Endocarp submedian, woody, 13 mm long.

Distribution - Papua New Guinea, endemic.

Habitat - Primary forest in hilly and submontane areas.

Note – Merrill & Perry founded this species on the first two Brass collections. I see no strong characters that distinguish the collection which had been annotated as a new species by St. John; it is unfortunate that this and other unpublished binomials tend to be published as nomina nuda.

PAPUA NEW GUINEA — Western Prov.: Wassi Kussa R., Tumbuke, common in rain forest on a fresh-water creek, Dec. 1936, *Brass 8487* (A, holotype); Oriomo R., Dagwa, not uncommon in low timber belts along creeks, at 40 m alt., 16 Feb. 1934, *Brass 5942* (A). — Milne Bay Prov.: Maneau Range, Mt Dayman, N slope, gully in oak forest, 800 m alt., July 1953, *Brass 23461* (LAE, *'maneauensis'*).

3. Pandanus microdontus Merr. & Perry

Pandanus microdontus Merr. & Perry, J. Arnold Arbor. 20 (1939) 177, pl. 1, f. 18; St. John, Pacif.
 Sci. 14 (1960) 227; Stone, Bot. Jahrb. 94 (1974) 497; Huynh, Bot. Jahrb. 97 (1976) 94. —
 Type: Brass 7695, Papua New Guinea.

Stem unbranched, 3-4 m long, on a few erect crowded stiltroots 20-30 cm long. Leaves c. 275-300 cm long, 6.8-8.5 cm wide, acute, scarcely acuminate. Margins near base prickly from about 15 cm above the base with comparatively small, rather widely spaced prickles 1.5-2 mm long, 2-6 mm apart, slender, spreading, antrorse; at the middle, the prickles antrorsely curved, 1 mm long, 7-17 mm apart; near apex the prickles 0.5 mm long, alternating with smaller prickles about half as long, 1-4mm apart. Apical ventral pleats with short antrorse prickles 0.5-0.75 mm long, 2-10 mm apart or more, irregularly spaced, along the distal 45 cm of the blade. Longitudinal veins about 143-145 per leaf. *Pistillate cephalium* solitary, oblong, about 25 cm long, 8 cm wide, composed of numerous pink drupes each c. 20 mm long, 4 mm wide, narrowly cuneate, apex obtuse, subtruncate, pileus 3 mm high, subconcave, the style subexcentric, dentiform to flabelliform. Mesocarp fibrous, 5-7 mm long. Endocarp 6-7 mm long, bony.

Distribution – Papua New Guinea, endemic; known only from the type locality. Habitat – Occasional in rain forest (low altitude).

Note – Merrill and Perry suggested an affinity with *Pandanus kivi* Martelli, but that species is here regarded as synonymous with *P. tabbersianus* Rendle, and is a

small, slender stemmed plant with smaller leaves and drupes and a pale yellow pericarp.

PAPUA NEW GUINEA — Lake Daviumbu: Middle Fly R., Sep. 1936, Brass 7695 (A, holotype).

4. Pandanus beccarii Solms-Laubach – Figs. 1–4

- Pandanus beccarii Solms-Laubach, Ann. Jard. Bot. Buitenzorg 3 (1883) 97; Warburg; Pflanzenr. Heft 3 (IV, 9) (1900) 71, f. 20A-D; Martelli, Webbia 4 (1) (1913) 7; 4 (2) (1914) t. 28, f. 20-25; Merr. & Perry, J. Arnold Arbor. 20 (1939) 181; St. John, Pacif. Sci. 14 (1960) 227; Stone, Bot. Jahrb. 94 (1974) 497; Huynh, Bot. Jahrb. 97 (1976) 92. Type: Beccari s.n., 1873, Aru Islands.
- Pandanus floribundus Merr. & Perry, J. Arnold Arbor. 20 (1939) 181, pl. 1, f. 19. Type: Brass 6975, New Guinea.
- Pandanus aprilensis St. John, Pacif. Sci. 27 (1973) 62, f. 310. Type: Ledermann 8756, New Guinea.

Pandanus clausus St. John, Pacif. Sci. 27 (1973) 69, f. 313. — Type: Clemens 171, New Guinea. Pandanus daulos St. John, nom. ined. in herb.; ex Huynh, Bot. Jahrb. 97 (1976) 93, nom. nud. Pandanus perryae St. John, nom. ined. in herb.; ex Huynh, Bot. Jahrb. 97 (1976) 92, nom. nud.

Robust tree with stout trunk, branched above into a small crown, about 15 m tall, with many crowded, basal, nearly erect, somewhat prickly proproots. Leaves large, to c. 400 cm long, about (6-)7.5-11.2 cm wide, acute. Sheathing base unarmed along lower 13 cm, the margins thereafter with crowded prickles 1-2.5 mm long, 1-5 mm apart; near middle with prickles slightly longer, 7-11 mm apart; near apex, the prickles slightly shorter, 1-4 mm apart. Midrib near the base with prickles 1-1.5 mm long, antrorse or laterally deflected, 1-6 mm apart; near middle small, 1 mm long; near apex 0.7-1 mm long, crowded. Lower surface of blade somewhat glaucous, upper surface dark green. Apical ventral pleats sparsely antrorsely prickly, or sometimes unarmed. Pistillate cephalium terminal, solitary, ovoid-cylindric, 30-45 cm long, (7-)11-14 cm wide, subtrigonous, red when ripe, sheathed closely in the adherent persistent bracts, long-pedunculate and composed of very numerous drupes. Drupes red, apex darker or purplish, 20-22(-28) mm long, 4-6(-8) mm wide, the pileus 2.5–4 mm high, truncate or slightly rimmed, stylar turret subcentral, slightly elevated, flat-topped, the stylar visor excentric, small, deltoid-sagittate to obscurely bilobed; stigma about 1 mm wide or less. Endocarp median, bony, brown, c. 9 mm long, the walls 0.25-0.5 mm thick. Staminate inflorescence a large compound pendulous spadix with 7 or 9 spikes and about 13 sterile bracts, peduncle somewhat zigzag, overall about 150 cm long, c. 2.5 cm thick, the sterile bracts up to 140 cm long and 11 cm broad, the fertile bracts about 45–50 cm long, 9–10 cm wide, or smaller. Spikes oblong, c. 20 cm long, 2.5 cm thick, dull cream or yellowish; staminal phalanges numerous, crowded; filaments almost free, bulbous, 0.35 mm long, rounded; pendiculus about equal, filiform; anther oblong, c. 2 mm long, including the 0.24 mm long apiculus.

Distribution - New Guinea and the immediately adjacent Aru Islands.

Habitat - Swamp forest and rain forest from lowlands up to c. 1600 m alt.

Note – In reducing *Pandanus floribundus*, *P. aprilensis*, and *P. clausus* I adopt a rather wide concept of this species, to which I have added specimens annotated in herbaria as new taxa with names that have not been validly published. Huynh has



Fig. 1. *Pandanus beccarii* Solms-Laubach. Vegetative structures (from *LAE 53082*). A: leaf base, dorsal surface; B: portion of leaf middle, dorsal surface; C: leaf apex, ventral surface; D: segment of proproot showing rows of spines; E: segment of branch below leaf crown, showing scattered spines. Drawn by Terry Nolan; Lae Herb. illustr. no. 1025, courtesy of LAE.



Fig. 2. *Pandanus beccarii* Solms-Laubach. Fruit head, outer bract, and inner bract (from *LAE 53082*). A: outer bract; note gap in marginal serration; B: inner bract; C: cephalium, with one outer bract, the fruit at apex cut away to show the receptacle and drupes. Drawn by Terry Nolan; Lae Herb. illustr. no. 1028, courtesy of LAE.



Fig. 3. *Pandanus beccarii* Solms-Laubach. Details of ripe drupes (from *Lae 53082*). A: drupe (fresh) in profile; B: another drupe, in oblique view from above; C: drupe in profile, another face; D: drupe in top view, showing stylar turret, stylar visor and (in heavy black) the slightly lobed stigma; E: drupe in longitudinal section; seed chamber in black; note upper mesocarp fusiform fibers. F: drupe in transverse section; endocarp in black; mesocarp fibers in white; seed and placenta shown in central chamber. Drawn by Terry Nolan; Lae Herb. illustr. no. 1031, courtesy of LAE.



Fig. 4. *Pandanus beccarii* Solms-Laubach. Staminate inflorescence and details (from *LAE 53082-B*). A: entire staminate spadix; B: small segment of staminate spike with 6 stamens; note filiform pendiculi and bulbous filaments, basal connections inconspicuous; C: pollen; a random group of 5 grains embedded in pollenkitt. Drawn by Terry Nolan; Lae Herb. illustr. no. 954, courtesy of LAE.

cited some of these in his anatomical studies but they are still *nomina nuda*. There is at least one other such *in scheda* name which I hope will remain unpublished. The differences to be seen in these specimens seem mainly a function of the vicissitudes of collecting and preservation of material, and not characters of actual taxa; among them are very small differences of drupe length, pilear height, and leaf width and length. The description of the staminate inflorescence is based on *LAE 53082-B* which is correlated with a pistillate plant (*LAE 53082*) growing next to it in the Botanic Gardens in Lae and similar in all respects.

INDONESIA — Aru Islands, Tjabu Lengan, Apr. 1873, O. Beccari (FI, holotype). A superb. pencil drawing of the fruit, drupes, and leaf, prepared by Martelli's artist, is preserved also in FI.

PAPUA NEW GUINEA — Western Prov.: Kiunga, 100 ft alt., 7 Aug. 1971, Streimann LAE 51748 (L, LAE); Ihu, Vailala R., 26 Apr. 1971, Stone & Galore LAE 53328, 53371 (LAE). — Rabaraba Subdistr., Ugat and Mayu Rivers junction, 350 m alt., 29 June 1972, Streimann & Katik NGF 28615 (L, LAE); Same locality, 450 m alt., 17 July 1972, Streimann & Katik NGF 28926 (L, LAE); Palmer R., 2 mi below junction of Black R., riverine forest at 100 m alt., June 1939, Brass 6975 (A, holotype of P. floribundus). — Ferguson Island: Mt Kilkerran, Woiatabu, 1200 m alt., 8 Dec. 1976, Croft LAE 71058, 71059 (LAE). — Milne Bay Prov.: Goodenough Island, E slopes, 1570–1600 m alt., 8–15 Oct. 1953, Brass 24639 (A, L, LAE; 'daulos' ined.). — Morobe Prov.: Sattelberg Range, 3000 ft alt., 20 Sep. 1935, Clemens 171 (L, holotype of P. clausus). Lae: Botanic Garden, 28 Mar. 1971, Stone LAE 53082, 53082-B (KLU, L, LAE). Aprilfluss (April R.): Standlager alluvialwald 40–60 m alt., 17 Sep. 1912, Ledermann 8756 (B, holotype of P. aprilensis).

5. Pandanus cernuifolius Merr. & Perry

Pandanus cernuifollus Merr. & Perry, J. Arnold Arbor. 20 (1939) 180, pl. 1, f. 20; Stone, Bot. Jahrb. 94 (1974) 497; Huynh, Bot. Jahrb. 97 (1976) 92. — Type: Brass 3916, New Guinea.

Stem c. 3-4 m tall, c. 4 cm diam. Proproots basal, few, short, with scattered stout prickles. Leaves 125-215 cm long, 4.4-5.3 cm wide, acute, subacuminate. Margins near base with prickles beginning about 5-6 cm beyond end of sheath, 1-2 mm long, 3-12 mm apart; near middle small, appressed, 0.5 mm long, 3-6(-more) mm wide; near apex the prickles 0.5-0.7(-1) mm long, 1-3 mm apart. Midrib near base unarmed, rounded, but along distal third with prickles 0.5 mm long, 4-5 mm apart, more or less similar to those of adjacent margin. Apical ventral pleats with antrorse, rather remote, small prickles along the distalmost 15-35 cm. Pistillate cephalium solitary, pendulous, only immature head seen, this 8 cm long, 4 cm wide. Drupes 16 mm long, 3 mm wide; pileus subimpressed to truncate or low convex, stylar turret central, horizontal, 1 mm high, with the stigma small, slightly lobed. Pericarp orangebrown with glaucous bloom. Staminate inflorescence to c. 40 cm long, with bracts 10-25 cm long, narrowly ovate navicular, acute-acuminate, margins and keels (especially distally) minutely ciliolate-spinulose. Spikes 7 (or 9?), about 7 cm long, 1.5 cm thick, the axis 2.5-3 mm thick when dry. Staminate flowers with bulbous filaments 1.75 mm long; pendiculus 0.25-0.3 mm long; anther 2.75 mm long, 0.5 mm wide; apiculus 0.25-0.3 mm long.

Distribution – New Guinea, both Irian and Papua New Guinea, endemic. Habitat – Rain forest, 500–1200 m alt.

Note – As noted by Merrill and Perry the leaves of this species resemble those of *P. krauelianus*.

INDONESIA — West Irian: Nassau Mts, 900 m alt., Oct. 1926, *Docters van Leeuwen 10572* (L, staminate); Idenburg R., Bernhard Camp, 6 km SW, in oak forest undergrowth, 1200 m alt., Feb. 1939, *Brass 12875* (A, L).

PAPUA NEW GUINEA --- Central Prov.: Ononge Rd, Dieni, 500 m alt., 1 May 1953, Brass 3916 (A, holotype; BRI).

6. Pandanus croceus B.C. Stone

Pandanus croceus B.C. Stone, Contrib. Herb. Austral. 4 (1974) 23, figs. 9–11; Bot. Jahrb. 94 (1974) 497; Huynh, Bot. Jahrb. 97 (1976) 92. — Type: Stone LAE 53590, Manus, Admiralty Islands.

Tree to 15 m tall, clear bole 5-8 m tall; branches few, dichotomizing sparsely; trunk at base with narrow cone-like array of proproots to 2 m long, 5 cm diam., with lines of short, blunt, rather distant protuberances. Bark of trunk greyish, comparatively smooth. Leaves (of vigorous juvenile plants) to 400 cm long, 12 cm wide; (of adult plants) usually 200-300 cm long, 7-10 cm wide; upper surface dark green, lower surface grayish-bluish glaucous; apex attenuate acute, not or scarcely acuminate. Blade margins near base with small, antrorse, straight or slightly curved, crowded prickles scarcely 1 mm long or less, 1-1.5 mm apart; near middle the prickles more appressed and sharper, acicular, slightly more distant; near apex still more slender, more crowded, usually 1-2 mm apart. Midrib near extreme base smooth, and from 20-30 cm beyond with minute, erect, deltoid, crowded prickles 0.5 mm long, 1-3 mm apart; near middle with similar but antrorse and more acicular prickles; near apex, with prickles similar in size and spacing to those of adjacent margin, but the ultimate 2-3 cm with midrib unarmed. Pistillate cephalium terminal, solitary, pendulous, sheathed in bracts, the outer series foliaceous-tipped, basally expanded, purplish-glaucous; inner bracts navicular, salmon- or coral-pink; innermost bracts linear; all midribs and margins finely serrulate. Cephalium narrowly conoid-cylindroid, 28-41 cm long, 8.5-13 cm diam., the peduncle 28-36 cm long, 4-5 cm thick, flared at apex, trigonous. Drupes yellow to pale yellow-orange when ripe, 13 mm long, 4-5 mm wide, the pericarp slightly firm-fleshy, with parallel sides, 5- or 6-angled; pileus low, flat, 1 mm high, central turret rather obscurely demarcated as a 5- or 6-angled rim, centrally somewhat concave; stylar visor usually 2-toothed (sometimes 1- or 3toothed), overtopping the small black stigma. Upper mesocarp fleshy fibrous, 3-3.5 mm long; lower mesocarp 3 mm long. Endocarp central, ellipsoid, 6 mm long, wall reddish bony, 0.5 mm thick; seed ellipsoid, 4.5-4.9 mm long, 2 mm wide. Staminate inflorescence large, pendulous, with 15-17 bracts, outer ones purplish glaucous, inner ones salmon-pink; spikes white and orange, to 18 cm long, 2-2.5 cm wide, of numerous staminate flowers with the filaments almost completely free, each filament clavoid bulbous, 2.5 mm long, abruptly contracted at the junction with the 0.5 mm long white pendiculus; anther linear-oblong, 2.75 mm long, with a short, white, acute apiculus 0.4 mm long.

Distribution - Papua New Guinea: Admiralty Islands; Manus Island.

Habitat – On limestone and other soils, from near sealevel to about 500 m alt. Vernacular name – Rei.

Note – The combination of yellow pericarp, very short drupes, thick receptacle, and essentially free filaments (no staminal tube) is the key set of diagnostic features of this species.



Fig. 5. *Pandanus krauelianus* K. Schum. Leaf apex, and fruit details (from *Brass 32315*). Drawn by B.C. Stone from a specimen in US.

PAPUA NEW GUINEA — Admiralty Islands. Manus Island: hills above Lorengau, 150 ft alt., 18 June 1971, Stone 10290 = LAE 53590 (LAE, holotype); 100 ft alt., same date, Stone 10294 = LAE 53594 (LAE, staminate infl.); SW Manus near Kabuli Village, 50 ft alt., 22 June 1971, Stone 10394 = LAE 53694 (LAE), 10395 = LAE 53695 (LAE, staminate infl.).

7. Pandanus krauelianus K. Schum. - Figs. 5 & 6

Pandanus krauelianus K. Schum. in K. Schum. & Hollrung, Fl. Kaiser-Wilhelmsland (1889) 17;
Warburg, Pflanzenr. Heft 3 (1900) 72; Martelli, Webbia 4 (1) (1913) 19; 4 (2) (1914) t. 28, f. 4-6; Merr. & Perry, J. Arnold Arbor. 20 (1939) 178; Kanehira, Bot. Mag. Tokyo 54 (1940) 254; St. John, Pacif. Sci. 14 (1960) 227; Stone, Bot. Jahrb. 94 (1974) 497; Huynh, Bot. Jahrb. 97 (1976) 93. — Type: Hollrung 164, New Guinea.

Pandanus beccarii sensu K. Schum., Bot. Jahrb. 9 (1888) 192, non Solms, 1883.

Pandanus flabellistigma Martelli, Webbia 1 (1905) 366, p.p., excl. descr. fol.; 4 (1) (1913) 19; 4 (2) (1914) t. 28, f. 7-10 (fide Martelli). — Type: Kurz, Hort. Bot. Buitenzorg (CAL).

Pandanus nakanaiensis B.C. Stone, Melan. Pl. Stud. I & Micron. Suppl. 1 (1965) 2. — Type: Floyd NGF 6440, New Britain.

Pandanus flexibilis St. John, nom. ined. in herb.; ex Huynh, Bot. Jahrb. 97 (1976) 93, nom. nud. Pandanus wauensis St. John, nom. ined. in herb.; ex Huynh, Bot. Jahrb. 97 (1976) 93, nom. nud.

Slender trees 3-8 m tall, branched above, trunk below raised on few or many fluted thorny proproots to 2.5 m long. Leaves narrowly linear, 160–180 cm long, 3.2–3.8 cm wide, narrowly sheathing, apex attenuate-acuminate into a subcaudate tip 2-4 cm long and 3 mm broad at a point 5 cm below the apex, 10 mm broad at a point 10 cm below the apex; texture at base rigid, distally pliant coriaceous to thin subcoriaceous. Margins armed along their entire length, near base with stiff deltoid prickles spreading or erect or slightly antrorse, 1 mm long, slender, sharp, close, about 1.5-1.75 mm apart; near middle with prickles strongly antrorse to appressed, similar in size but more distant, 2-5 mm apart; near apex the prickles much smaller, 0.5 mm long or less, appressed, densely crowded, weak, about 1 mm apart or less; larger and smaller prickles often present, alternating. Midrib beneath unarmed toward the base, distally along the last quarter with minute, appressed, antrorse prickles like those of adjacent margins but somewhat more distant. Apical ventral pleats sparsely and irregularly armed (or not infrequently smooth and unarmed), with very few, minute, appressedantrorse prickles no larger than those of adjacent margin, often present sporadically only about 10-20 cm below apex. Blades more or less glaucous beneath; when dry pale dull grey-green beneath. Pistillate cephalium solitary, pendulous, smallish, on a peduncle c. 15-20(?) cm long, at apex to 2 cm broad, with 15-21 ovate navicular bracts, these at apex briefly acuminate, their margins densely minutely spinulosedenticulate; midrib dorsally raised, unarmed except for few minute prickles near apex; texture coriaceous and somewhat rigid, striate longitudinally when dry, ventrally smooth or obscurely striate; outermost 3-5 bracts on peduncle, 5-15 mm apart; inner ones from base of cephalium and closely enveloping it, the outer larger ones slightly longer than the cephalium, the innermost much shorter and almost linear. Cephalium narrowly ovoid, apically rounded, basally rounded-subtruncate, obscurely trigonous, of many crowded drupes. Drupes 21-24 mm long, 7-9(-10) mm wide, 5- or 6-angled, yellow to palest orange when ripe; pileus brownish, 1-2 mm high, centrally shallowly concave, with definite but almost obsolete ridges running



Fig. 6. *Pandanus krauelianus* K. Schum. Details of staminate inflorescence (from *Kairo 748*). Spike; segment of longitudinal section of spike with staminal flowers with distinct staminal tubes; detail of 10 staminal flowers in transverse section through the filaments; single stamen with filament, pendiculus, and anther; detail of anther apex showing raphidophorous cells in apiculus. Drawn by B.C. Stone from a specimen in PH.

out to the corners; stylar visor slightly adaxially excentric, appressed, 1–1.5 mm wide, 2–4- (usually 3-)toothed, overtopping the small dark stigma. Upper mesocarp fleshy fibrous, the conspicuous fusiform fibers 0.2 mm diam. apically crossed by pithy plates. Endocarp central, ellipsoid-fusiform, bony, dark brown, 10–11 mm

long, outer light colored layer 0.3 mm thick, inner dark layer 0.5 mm thick. *Stami*nate inflorescence terminal, pendulous, 35-40 cm long, with about 13 bracts of which 5 fertile, salmon pink to apricot colored, stiff, concave, navicular, the longer ones to 28 cm long, 6.5 cm wide, at apex rounded, not apiculate, the margins finely serrulate. Spikes to 17 cm long, 2 cm wide, yellow. Staminal flowers (phalanges) numerous, the filaments 2–2.5 mm long, narrowly clavoid; pendiculus 0.25–0.75 mm long; anthers yellow, oblong, (2-)2.25-3.25 mm long, including the short 0.25–0.33 mm long apiculus. Pollen yellow.

Distribution - New Guinea, Bismarck Archipelago (New Britain), endemic.

Habitat – Rain forest understorey, at low or moderate altitudes (to c. 1200 m), on various (sometimes heavy clayey) soils.

Notes – From Martelli's account of his *Pandanus flabellistigma*, most of the protologue must apply in reality to *P. amboinensis* Warb. Martelli cites *P. ceramicus* Kurz as a synonym; this is, however, *P. conoideus* (sensu auctt., non Lamk.). In 1913, Martelli reduced his *P. flabellistigma* to *P. krauelianus*.

This species is one of the more common in New Guinea, at least in the areas where I have actually collected, and is rather distinct and readily recognised.

Merrill and Perry thought that *P. kivi* Martelli might be synonymous; here, however, that species is regarded as a synonym of *P. tabbersianus* Rendle (see below). The specimen cited, however, appears to be *P. krauelianus*.

PAPUA NEW GUINEA --- Morobe Prov.: "Kaiser-Wilhelmsland, an Flussufern", Hollrung 164 (B, holotype; FI); Oomsis, 200 m alt., 25 Apr. 1959, Brass 29252 (A, 'reconditus'); Lowe's Ford, Kassam-Water Rice Rd, gallery forest, 540 m alt., 30 Oct. 1959, Brass 32315 (A, 'flexibilis'); Bulolo-Middle Creek Rd, 45 mi, 1000 m, 18 Mar. 1971, Stone 9736 = LAE 53036 (LAE); Bulolo, Humps Head Rd, 32 mi, 1000-1150 m alt., 17 Mar. 1971, Stone 9724 = LAE 53024 (LAE, staminate infl.); SE of Bulolo 9 km, 1180 m alt., 20 Feb. 1980, Kairo 748 (LAE, PH, staminate infl.); Bulolo, on Lae-Wau Rd, creek rain forest, 850 m alt., 17 Jan. 1958, St. John 26220 (BISH, LAE); Lae-Bulolo Rd, 20 mi from Lae, 100 m alt., 19 Mar. 1971, Stone 9763 = LAE 53063 (LAE); Markham Valley, Kajabit, 9 Aug. 1939, Clemens 10568-A (A, UC); Markham Point, 180 m alt., 25 Feb. 1972, Streimann NGF 24424 (LAE, staminate infl.); Wau, N slope Watut Valley, 1150 m alt., 1 June 1967, Womersley NGF 24963 (LAE, 'wauensis'). - Lae: Botanic Gardens, 24 June 1959, Henty NGF 10656 (LAE, staminate infl.); 5 May 1971, Stone 10148 = LAE 53448 (LAE); 20 July 1971, Stone 10510 = LAE 53810 (LAE, staminate infl.). — Western Highlands Prov.: Jimi Subdistr., Koenambe, 650 m alt., 12 Oct. 1970, Clarke ANU 9606 (LAE). - Central Div.: Dieni, Ononge Rd, 500 m alt., Apr.-May 1933, Brass 3851 (A); Fly R., 528 Mile Camp, 80 m alt., 1936, Brass 6764 (A); Middle Fly R., Lake Daviumbu, 1936, Brass 7518 (A).

BISMARCK ARCHIPELAGO — New Britain: near Cape Hoskins, West Nakanai, Galilo Village, 4 Aug. 1954, *Floyd NGF 6440* (LAE, type of *P. nakanaiensis*).

8. Pandanus tabbersianus Rendle ex Gibbs

Pandanus tabbersianus Rendle ex Gibbs, Dutch New Guinea (1917) 198; Stone, Bot. Jahrb. 94 (1974) 497. — Type: Gibbs 6213, Dutch New Guinea, i.e. West Irian.

- Pandanus kivi Martelli, J. Arnold Arbor. 10 (1929) 140; White, J. Arnold Arb. 10 (1929) 202;
 Merr. & Perry, J. Arnold Arbor. 20 (1939) 178; Huynh, Bot. Jahrb. 97 (1976) 93. Type:
 Brass 1557, New Guinea.
- Pandanus biformatus, St. John, Pacif. Sci. 27 (1973) 67, f. 312; Huynh, Bot. Jahrb. 97 (1976) 93. — Type: Brass 23765, New Guinea.

Pandanus imbrialis St. John, nom. ined. in herb., ex Huynh, Bot. Jahrb. 97 (1976) 93, nom. nud.



Fig. 7. Pandanus amboinensis Warb. Details of staminate inflorescence (from *de Vriese 171*). Segment of spike with most anthers omitted, and a zone with staminal flowers removed; at right, detail of apiculus and a single stamen. Drawn by B.C. Stone from the holotype (L).



Fig. 8. Pandanus amboinensis Warb. Drupes in profile, top view, and longitudinal section (from C.B. Robinson 31). Drawn by B.C. Stone, from specimen in L.

Tree 5-10 m tall; trunk spiny; propoots spiny. Leaves 140-300 cm long, 4.2-6.4 cm wide, linear-attenuate, apex narrowly acute. Margins near base with spreading narrowly deltoid prickles 1.3–1.8 mm long, crowded 0.5–2 mm apart, alternately longer (1.6 mm) and shorter (1 mm); at the middle with prickles more appressed, 1 mm long, mostly 2-4 mm apart: near apex the prickles appressed-antrorse, 0.4-0.9 mm long, alternately longer and shorter, about 1.5 mm apart; at extreme tip 0.5 mm long, sharp and brown-tipped. Lower surface of blade somewhat glaucous. Longitudinal veins closely set (0.35 mm apart), 150-160 per leaf. Midrib near base unarmed, smooth; near the middle closely prickly, the prickles short, blunt, 0.5 mm long, 2 mm apart; toward apex prickles short, antrorse, less than 0.5 mm long, 2-4 mm apart. Apical ventral pleats sparsely prickly or (sometimes) unarmed. Pistillate cephalium solitary, terminal, elongated cylindric-ellipsoid, peduncle stout, 35 cm long, 2 cm thick near apex. Bracts closely enveloping, 60-70 cm long, almost 10 cm wide, the margins finely denticulate-serrulate with prickles 1 mm long, 1 mm apart, near base alternately longer and shorter, longer ones almost 2 mm long; midrib dorsally unarmed along basal third, thereafter with closely appressed antrorse prickles 1 mm long, 1-2 mm apart. Cephalium 40-41 cm long, 9-9.5 cm wide, composed of very numerous drupes. Drupes 18-21 mm long, 4-5 mm wide; pileus 2-2.5 mm high, low convex, slightly concave; stylar turret almost nil, stylar visor excentric; 1-1.3 mm wide, bidentate. Endocarp 13 mm long, 4 mm wide.

Distribution – New Guinea and immediately adjacent islands (Sudest, Fergusson, Normanby), endemic.

Habitat - Rain forest at low altitudes.

INDONESIA — West Irian: Manokwari, track to Ambani, 30 m alt., forest edge, Jan. 1914, Gibbs 6213 (BM, holotype).

PAPUA NEW GUINEA — West of Wewak 15 mi, Awain, 29 Dec. 1957, St. John 26183 (A). — Central Div.: Kubuna, 100 m, Nov. 1933, Brass 5655 (A, LAE, 'imbrialis'). — Eastern Div.: Lower Mori R., 28 May 1926, Brass 1557 (A, isotype of P. kivi). — Milne Bay Prov.: Gwariu R., Biniguni camp, in rain forest, 200 m alt., 2 Aug. 1953, Brass 23765 (K, holotype of P. biformatus, A, LAE). — Sudest Island: Rambuso, ridge rain forest, 30 m alt., Brass 28120 (PNH, 'bidrupaceus'). — Fergusson Island: Agamoia, 22 June 1956, Brass 27272 (A, PNH, 'auritus'). — Normanby Island: Waikaiuna, 20 m alt., 15 Apr. 1956, Brass 25446 (A, PNH).

9. Pandanus amboinensis Warb. - Figs. 7-9

Pandanus amboinensis Warb., Pflanzenr. Heft 3 (IV, 9) (1900) 83; Martelli, Webbia 4 (1) (1900) 6;
 4 (2) (1914) t. 26, figs. 17–19; Merr., Interpret. Rumph. Herb. Amboin. (1917) 82; Stone, Bot. Jahrb. 94 (1974) 497; Huynh, Bot. Jahrb. 97 (1976) 92. — Type: De Vriese 171, Amboina.

Pandanus silvestris Rumph., Herb. Amboin. IV (1743) 145, t. 77. — P. sylvestris Kunth, Enum. 3 (1841) 98; non Bory, 1804.

Pandanus luteus St. John, Pacif. Sci. 27 (1973) 77, figs. 318, 319; Huynh, Bot. Jahrb. 97 (1976)
 93. — Type: Brass 23191, Goodenough Island, New Guinea.

Pandanus biciliatus St. John, Pacif. Sci. 27 (1973) 64, f. 311; Huynh, Bot. Jahrb. 97 (1976) 93. — Type: Brass 28746, Woodlark Island, New Guinea.

Tree 6-12 m tall, branched above, trunk on stilt-roots. Leaves to at least 180 cm long, 5.5–7.4 cm wide, deeply channelled above toward base, sheathing base 5-10 cm long, stiff-coriaceous. Margins near base closely and regularly prickly, the most

proximal prickles minute, less than 0.5 mm long, blunt, crowded, 0.5 mm apart, thereafter successively longer, to 1.5-2 mm long, sharp, somewhat spreading antrorse, dark-tipped, 1 mm apart, rather unequal, with some alternating shorter and longer prickles; near middle, the prickles antrorsely curved, subappressed, 1 mm long, 1-2 mm apart; near apex, the prickles similar but more slender, unequal, larger ones (1 mm long) alternating with smaller ones (0.5 mm long), sometimes two long ones followed by one or two short ones (the second one of a pair sometimes partly joined to its neighbour). Midrib near base entire, rounded, smooth, but from about 30 cm above base set with small antrorse prickles 0.6-0.7 mm long, on the slightly raised keel, 2-3 mm apart; toward apex, the prickles more crowded, appressed, scarcely 1 mm apart. Apex attenuate acute, slightly acuminate. Upper surface somewhat dark subglossy green; lower surface glaucous pale, finely striate by the c. 150 longitudinal veins, these closely set (c. 0.33 mm apart). Apical ventral pleats with a few small, irregularly spaced, often rather distant prickles, these sometimes obsolete or even lacking. Pistillate inflorescence terminal, solitary, pendulous, on a stout re-



Fig. 9. Pandanus amboinensis Warb. Leaf apices, dorsal and ventral views (from Beguin 2314). Note alternation of larger and smaller prickles on margins; midrib prickles slightly more remote than marginal prickles; and extreme restriction of prickles on apical ventral pleat (only on one of the two pleats). Other leaves have these pleats unarmed.

curved peduncle at least 25 cm long, 15 mm wide, bracteate. Cephalium ellipsoidovoid, grayish-yellow, at anthesis about 17 cm long, 3.5 cm diam., enlarging and in fruit c. 35–42 cm long, 8–10.5 cm diam., composed of numerous drupes. Drupes short, oblong truncate, 5- or 6-angled, about 15–19 mm long, 4–6 mm wide; pileus 2.5–4 mm high, slightly concave to slightly convex; stylar turret low, flat, 1–1.125 mm long, stylar visor bilobed and obscurely trilobed. Endocarp central, ellipsoid, 10–13 mm long. Pericarp yellow. *Staminate inflorescence* with bracts to 45 cm long, 8 cm wide, narrowly ovate, navicular, apex somewhat prolonged, acute, margins spinulose prickly in distal half, the prickles rather unequal. Spikes 9 or 11, cylindric, 20–25 cm long, 7–10 mm wide, of many phalanges; stamens almost free; filaments 1.1–1.5 mm long, slightly bulbous, the surface with scattered raphidophorous cells; pendiculus c. 0.5 mm long; anther c. 3 mm long, including the acute 0.25 mm long apiculus, this dotted with raphidophorous cells. Distribution – Indonesia: Moluccas (Amboina, Halmaheira); New Guinea (W & E). Habitat – Lowland forest up to about 1570 m alt.

Notes – Although the species is first referred to by Rumphius, the publication by Warburg is the first valid name. Warburg used as his type the staminate collection from Amboina by De Vriese. The interpretation of Rumphius' Herbarium Amboinense by Merrill was facilitated by the new Amboina collections made by C.B. Robinson (who perished in the work). His collection no. 31 is of a pistillate inflorescence. Association by foliar characters of the two collections appears well justified. The specimens from New Guinea also seem to fit well. The peculiar alternation of large and small prickles on the leaf margins (emphasised by St. John in his descriptions) is seen both on the leaves and the bracts.

In Warburg's time the staminate characters of this group of species were not understood, and the nearly free stamens (virtually no staminal tube) led Warburg to assign *Pandanus amboinensis* to section *Acrostigma*. Today it is clear that this assignment was erroneous, and the species is manifestly a member of section *Maysops*. The only species of this section known to Warburg was *P. beccarii*, and that was known only by pistillate material. A similar decision was that of Martelli who assigned *P. pendulinus* to section *Acrostigma* for the same reason – the apparently free stamens. That species also has proved to be wrongly assigned, and Stone & Huynh (1983) showed that it belongs, if not to section *Maysops*, then to a very closely related (possibly new) section in subgenus *Lophostigma*.

INDONESIA — Amboina: H. de Vriese 171 (L, holotype, staminate infl.); C.B. Robinson 31 (L, pistillate). — Halmaheira: W. Tobelo, Berg Doekono, 800 m alt., 11 Dec. 1922, Beguin 2314 (L, staminate). — Pulau Rao Loleo, 50 m alt., 11 Dec. 1921, Beguin 1812 (L, pistillate flowers). — West Irian: Manokwari, dense forest, 10 m alt., 29 Nov. 1957, St. John 26116 (BISH, K).

PAPUA NEW GUINEA — Milne Bay Prov.: Maneau Range, Mt Dayman, 1550 m alt., moist hollows in oak forest, 29 June 1953, *Brass 23191* (LAE). — Goodenough Island: E slopes, mossy oak forest, 1570 m alt., 8–15 Oct. 1953, *Brass 24732* (K, holotype of *P. luteus*, LAE). — Woodlark Island: Kulumadau rain forest, 100 m alt., 14 Nov. 1956, *Brass 28746* (K, holotype of *P. biciliatus*, L, US).

10. Pandanus concavus St. John - Fig. 10

Pandanus concavus St. John, Pacif. Sci. 27 (1973) 71, figs. 314-316; Stone, Bot. Jahrb. 94 (1974) 497; Huynh, Bot. Jahrb. 97 (1976) 93. — Type: Kalkman 4416, W New Guinea.

Tree to 14 m tall, branched above, with aculeate proproots to 4 m long. Leaves to c. 200 cm long, 7 cm wide, rigidly coriaceous, pale or subglaucous beneath, linear, gradually attenuate-subacuminate. Margins near base with spreading prickles 0.8-1.7 mm long, 2-3 mm apart; near middle with prickles about the same length but 4-7 mm apart; near apex the prickles noticeably unequal, larger ones alternating with smaller ones, the longer ones to 1 mm long, the shorter to 0.6 mm long, all 0.5-2 mm apart. Midrib beneath unarmed proximally, thereafter with prickles like those of adjacent margins. *Pistillate inflorescence* terminal, solitary, pendent, the peduncle (in fruiting state) c. 50 cm long, the outer bracts lanceolate, navicular, coriaceous, to 12 cm wide (flattened), the margins ciliate. Cephalium 38-48 cm long, 5.6-8 cm diam., subcylindric, composed of numerous simple red drupes. Drupes 14-15.5 mm long,



Fig. 10. Pandanus concavus St. John. Leaf and drupe details (from Kalkman 4416). A: leaf base, dorsal surface; B: leaf middle segment, dorsal surface; C: leaf apex (tip broken off), ventral surface; D: drupe in profile; E: drupe in longitudinal section; F: drupe in top view, stigma on the right; G: drupe in transverse section. Drawn by Terry Nolan; Lae Herb. illustr. no. 1244, courtesy of LAE.

3.5-7 mm wide, prismatic, 5-6-angled, the upper 1/7th free, subtruncate, pileus 2 mm high, somewhat concave, central turret to 2 mm high, the stylar visor and stigma mostly bidentate (rarely 1- or 3-toothed), 0.5-0.8 mm wide. Upper mesocarp densely fibrous. Endocarp in lower 2/5th of drupe, bony, brown, c. 9 mm long, seed chamber 2.5 mm wide.

Distribution – New Guinea (W and E), endemic.

Habitat -- In midmontane rain forest at about 1500-2000 m alt.

Vernacular name - 'Nort' (Sillitoe).

Note – In St. John's fig. 314 m (leaf apex) it should be noted that the rather abruptly acute tip shown is that of a foliaceous bract or scale leaf, not that of a normal adult leaf, which has a much more gradually attenuate-acuminate apex. (The difference is entirely normal, but the type of foliar organ needs to be specified in such cases.) The relationship of this species is probably with *Pandanus beccarii* (syn. *P. floribundus*) as suggested by the all red fruits, as already pointed out by St. John. Staminate plants remain unknown.

INDONESIA — West Irian: Mt Antares (Star Mts), E of junction with Bon and Minam Rivers, 1500 m alt., 13 July 1959, Kalkman 4416 (L, holotype).

PAPUA NEW GUINEA — Western Prov.: Kiunga Subprov., Ok Tedi region, 1460 m alt., June 1981, *Donoghue 11* (PH). — Southern Highlands Prov.: Nipa distr., Halalinja, 1950 m alt., early 1983, *Sillitoe 83-14-A* (PH).

11. Pandanus castaneus St. John & Stone - Figs. 11 & 12

Pandanus castaneus St. John & Stone in Stone, Melan. Pl. Stud. I & Micron. Suppl. (1965) 3; Bot. Jahrb. 94 (1974) 497; Huynh, Bot. Jahrb. 97 (1976) 92. — Type: Brass 32277, New Guinea.

Tree 7-9 m tall, branched above, elevated on a few short proproots to 1 m long. Juvenile plants with leaves to 4 m long, with the apical ventral pleats consistently prickly; adult leaves linear, drooping, about 190-280 cm long, 6-7 cm wide, deeply channelled above, lateral folds strongly arched, at apex shortly acuminate (acumen 1-3 cm long), upper surface green, lower surface slightly glaucous, base creamy pinkish. Margins near base with stout, crowded, spreading to erect prickles 2-2.5 mm long, about 2.5-3 mm apart; toward the middle the prickles more antrorse, somewhat more slender, or acicular, successively smaller, about 1-1.5 mm long, 5-20 mm apart; toward apex the prickles only 0.5 mm long, 1.5-2 mm apart. Midrib near base with a few blunt erect or almost retrorse prickles 0.5-1 mm long, 5-10 mm apart; near middle the midrib almost unarmed or with few, minute, scattered prickles; near apex the prickles similar to those of adjacent margins. Apical ventral pleats sparsely and irregularly prickly or more frequently unarmed. Pistillate inflorescence solitary, pendulous, the cephalium on a stout peduncle 24 cm long and 1.8 cm thick, the head cylindrical-ellipsoid, 19-23 cm long, 6-7 cm diam. at the middle, rounded-trigonous, sheathed by the c. 15 pallid yellowish navicular bracts, and below these about 3-6 subfoliaceous peduncular bracts over 100 cm long; inner bracts mostly 40 cm long or less, c. 12 cm wide, innermost 6-9 much shorter than cephalium, reduced to linear, the smallest $40 \times 4-5$ mm, all with densely denticulateserrulate margins (acicular prickles c. 1 mm long, 0.7-1 mm apart); midrib beneath distally with similar prickles. Cephalium rounded at both ends, composed of num-



Fig. 11. Pandanus castaneus St. John & Stone. Fruit, drupe details, and marginal prickles. Drawn by B.C. Stone from the holotype.

erous drupes. Drupes crowded, at first slightly adnate by the pericarps, later free, mostly 17– 20 mm long, 4-7(-10) mm wide; the fresh pericarp when ripe coral-red to pink-salmon, drying reddish-orange; pileus 1–1.5 mm high, without marginal rim, stylar turret central, 1– 1.5 mm wide, minutely bidentate, the stylar visor 1 mm high, subtruncate to slightly rounded; stigma small, dark, as wide as the stylar visor or slightly less. Mesocarp fleshy fibrous. Endocarp bony, 6.5 mm long, reddish, wall about 0.5 mm thick; seed chamber 5.5 mm long, 1.5 mm wide.

Distribution – Papua New Guinea, endemic. Habitat – Submontane rain forest, c. 900– 1400 m alt.

PAPUA NEW GUINEA — Western Highlands Prov.: 3 mi. from Lake Kopiago, 9 Nov. 1968, Vandenberg & Galore NGF 42085 (L, LAE). — Eastern Highlands Prov.: Morobe Distr., Kassam Pass, 900 m alt., 3 June 1971, Stone 10248 = LAE 53548 (KLU, LAE, PH); Kassam, 1370 m alt., 27 Oct. 1959, Brass 32277 (US holotype, A, L).



APPENDIX 1

12. Pandanus zea St. John

Pandanus zea St. John, Pacif. Sci. 14 (1960) 239, fig. 8; Huynh, Bot. Jahrb. 97 (1976) 94. — Type: Brass 19293, N Queensland.

Distribution - Australia, limited to N. Queensland.

Note – This species is now known by both pistillate and staminate materials, and has been fairly well collected and photographed. It appears to be similar to *Pandanus amboinensis*, *P. krauelianus*, *P. tabbersianus*, and *P. spodiophyllus*, but most closely perhaps to *P. tabbersianus*.

13. Pandanus flavicarpus B.C. Stone

Pandanus flavicarpus B.C. Stone, Melan. Pl. Stud. I & Micron. Suppl. 1 (1965) 2; Malays. J. Sci.
 1A (1972) 120, fig. 15; Bot. Jahrb. 94 (1974) 497; Huynh, Bot. Jahrb. 97 (1976) 92. — Type:
 Stone 2478, Solomon Islands.



Distribution – Solomon Islands (Santa Ysabel), endemic. Habitat – Lowland, muddy swamp with *Metroxylon* and *Cyrtosperma*.

14. Pandanus roseus B.C. Stone

Pandanus roseus B.C. Stone, Melan. Pl. Stud. I & Micron. Suppl. 1 (1965) 2; Malays. J. Sci. 1A (1972) 117, fig. 13; Bot. Jahrb. 94 (1974) 497. — Type: Stone 2559, Solomon Islands.

Distribution – Solomon Islands (Rendova Island), endemic. Habitat – Lowland rain forest, 33 m alt.

15. Pandanus rubellus B.C. Stone

Pandanus rubellus B.C. Stone, Melan. Pl. Stud. I & Micron. Suppl. 1 (1965) 2; Malays. J. Sci. 1A (1972) 118, fig. 15; Bot. Jahrb. 94 (1974) 497. — Type: Stone 2565, Bougainville.

Distribution – Bougainville Island; Buka Island; Guadalcanal Island; endemic. Habitat – Lowland swamp forest.

Note – Because of the political changes in Melanesia since 1960 the island of Bougainville has become part of Papua New Guinea, where formerly it was considered one of the Solomon Islands from a geographical viewpoint. Biogeographically as well as geographically it is intermediate. Since *Pandanus rubellus* as well as the other species noted here in this Appendix have been thoroughly treated with modern descriptions and citations, a full treatment here is unnecessary. *Pandanus rubellus* is similar to *P. beccarii* but has smaller leaves (c. 230×6.5 cm) with the apical ventral pleats rather densely and continuously prickly for a considerable distance along the apex.

16. Pandanus spodiophyllus B.C. Stone

Pandanus spodiophyllus B.C. Stone, Melan. Pl. Stud. I & Micron. Suppl. 1 (1965) 2; Malays. J.
 Sci. 1A (1972) 121, fig. 16; Bot. Jahrb. 94 (1974) 497; Huynh, Bot. Jahrb. 97 (1976) 94. —
 Type: Stone 2617, New Britain.

Distribution – New Britain, endemic.

Habitat – Lowland forest, 100–200 m alt.

Notes – New Britain is part of Papua New Guinea politically. *Pandanus spodiophyllus* does not appear to occur in mainland New Guinea. It has been fully described and illustrated recently in the above-mentioned publications. It is a species very close to *P. krauelianus* but slightly more robust with distinctly broader leaves (c. 210×6 cm), somewhat longer drupes (the lateral ones about 30 mm long), and a usually bidentate (not 2–4-toothed) stylar visor and stigma.

Another possible close relative is *P. cernuifolius*, but the available material of that species is too immature to provide a satisfactory comparison; however, the pericarp color seems to be the same. Also similar is *P. zea* of Queensland, which has perhaps slightly narrower leaves, shorter drupes (14–17 mm long), and the stylar visor 2–3-toothed.

APPENDIX 2

As earlier noted several nomina nuda have appeared in print; some are cited in synonymy above; some collections, however, have more than one name 'in scheda' according to the herbarium in which the various duplicates are preserved. The confusion arising from this practice is unfortunate. It would be useful if botanists would indicate on their annotation slips whether the name has or has not been validly published, and, if not, when and where the name is to be published.

- Pandanus auritus St. John, nom. ined.; ex Huynh, Bot. Jahrb. 97 (1976) 93. This is Pandanus tabbersianus Rendle.
- Pandanus bidrupaceus St. John, nom. ined.; ex Huynh, l.c. 93. This is Pandanus tabbersianus Rendle.
- Pandanus cernuus St. John, nom. ined.; ex Huynh, l.c. 92. The specimen so designated in herb. L is identified herein as Pandanus kosteri Stone.
- Pandanus daulos St. John, nom. ined.; ex Huynh, l.c. 93. This is Pandanus beccarii Solms-Laub.
- Pandanus flexibilis St. John, nom. ined.; ex Huynh, l.c. 93. This is Pandanus krauelianus K. Schum.
- Pandanus imbrialis St. John, nom. ined.; ex Huynh, 1.c. 93. This is Pandanus krauelianus K. Schum.
- Pandanus maneauensis St. John, nom. ined.; ex Huynh, l.c. 93. This is Pandanus xanthocarpus Merr. & Perry.
- Pandanus perryae St. John, nom. ined.; ex Huynh, 1.c. 92. This is Pandanus beccarii Solms-Laub.
- Pandanus reconditus St. John, nom. ined.; ex Huynh, l.c. 93. This is Pandanus krauelianus K. Schum.
- Pandanus wauensis St. John, nom. ined.; ex Huynh, l.c. 93. This is Pandanus krauelianus K. Schum.

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INDEX TO COLLECTION NUMBERS

Entries are alphabetically arranged by collector's name or series name in numerical order. The identification is indicated by the species numbers used in this paper and also given in the following list:

Pandanus

- 1. kosteri B.C. Stone
- 2. xanthocarpus Merr. & Perry
- 3. microdontus Merr. & Perry
- 4. beccarii Solms-Laubach
- 5. cernuifolius Merr. & Perry
- 6. croceus B.C. Stone
- 7. krauelianus K. Schum.
- 8. tabbersianus Rendle ex Gibbs
- 9. amboinensis Warb.
- 10. concavus St. John
- 11. castaneus St. John & Stone
- 12. zea St. John
- 13. flavicarpus B.C. Stone
- 14. roseus B.C. Stone
- 15. rubellus B.C. Stone
- 16. spodiophyllus B.C. Stone

ANU series: 9606 Clarke: 7.

Beccari Apr 1873: 4 — Beguin 1812: 9; 2314: 9 — Brass 1557: 8; 3851: 7; 3916: 5; 5655: 8; 5942: 2; 6764: 7; 6975: 4; 7518: 7; 7965: 3; 8487: 2; 12875: 5; 19293: 12; 23191: 9; 23461: 2; 23675: 8; 24639: 4; 24732: 9; 25446: 8; 27272: 8; 28120: 8; 28746: 9; 29252: 7; 32277: 11; 32315: 7.

- Clemens 171: 4; 10568-A: 7.
- Docters van Leeuwen 10572: 5 Donoghue 11: 10.
- Gibbs 6213: 8.
- Hollrung 164: 7.

Kairo 748: 7 --- Kalkman 4416: 10 --- Koster BW 6852: 1; BW 13646: 1 --- Kurz s.n. ex Hort. Bot. Buitenzorg: 7.

LAE series: 51748 Streimann: 4: 53024 Stone: 4: 53036 Stone: 4: 53063 Stone: 7: 53082 Stone: 4; 53328 Stone & Galore: 4; 53371 Stone & Galore: 4; 53448 Stone: 7; 53548 Stone: 11; 53590 Stone: 6; 53594 Stone: 6; 53695 Stone: 6; 53810 Stone: 7; 71058 Croft: 4 ; 71059 Croft: 4 - Ledermann 8756: 4.

NGF series: 6440 Floyd: 7; 10656 Henty: 7; 24424 Streimann: 7; 24963 Womersley: 7; 28615 Streimann & Katik: 4; 28926 Streimann & Katik: 4; 42085 Vandenberg & Galore: 11. Robinson 31:9.

Sillitoe 83-14-A: 10 — St. John 26116: 9; 26183: 8; 26220: 7. — Stone 2478: 13; 2559: 14; 2565: 15; 2617: 16 (other Stone numbers under the LAE series).