Pandanus subg. Martellidendron (Pandanaceae) part II: revision of sect. Martellidendron Pic. Serm. in Madagascar

M. W. CALLMANDER

Université de Neuchâtel, Institut de Botanique, Laboratoire de Botanique évolutive, Case postale 2, 2007 Neuchâtel 7, Switzerland

Received September 2000; accepted for publication February 2001

This paper provides a taxonomic revision of Pandanus sect. Martellidendron, which so far comprises six species of which only one is known from both staminate and pistillate plants. Research in herbaria and in the field in Madagascar has provided the data on which a revision of the unclear taxonomy of this section can be based. Based on micromorphology, architecture and phytogeography, the number of these dioecious species is reduced. One new species (l?gullinarum Callmander) from the Biosphere reserve of Mananara-North on the east coast is described, and l?lzaraka Martelli is transferred to this section 30 years after it was assigned to section Dauphinensia. A key to all species of subg. Martellidendron is provided. Finally, the important role of the section for the understanding of the phylogeny of the Pandanaceae is discussed in the context of Indian Ocean biogeography.


INTRODUCTION

The palaeotropical dioecious genus Pandanus comprises some 700 species of trees and shrubs divided into eight subgenera and 54 sections (Stone, 1974). Subg. Martellidendron comprises two sections: sect. Martellidendron described by Pichi-Sermolli in Martelli & Pichi-Sermolli (1951) which is endemic to Madagascar, and sect. Seychella described by St. John (1967), which is endemic to the Seychelles.

Subgenus Martellidendron is unique in the genus, and many morphological characters distinguish it from the other subgenera. These include:

1. The pollen grains, which have a reticulum with small lumina and a three-layered exine (Hotton, Leffingwell & Skvarla, 1994).
2. The anther structure, which has no endothecial thickenings in the lateral part of the connective and the proximal part of the anther walls (Huynh, 1983).
3. The endocarp, which does not extend between the seed locules, where it is replaced by the mesocarp extending from the apex to the base (Martelli & Pichi-Sermolli, 1951).
4. The constant numbers of stigmas (two), which are close and opposite, forming a cross in the apex of the pileus.

In contrast, nearly all the other subgenera have a twolayered exine, endothecial thickenings in the anther structure, a variable number of stigmas, and an endocarp that envelops the entire circumference of the seed locules, with a mesocarp only in the upper and basal part of the drupe.

Sect. Martellidendron appears to be a natural group comprising six Madagascan species. To date, only P. androcephalanthos Martelli is known from both staminate and pistillate plants (Martelli & Pichi-Sermolli, 1951). P. hermaphroditus Martelli and P. karriangensis Huynh are known only from staminate inflorescences, while P. cruciatus Pic. Serm., P. nosibicus Huynh and P. maoaensis Laivao & Callmander are known from the pistillate.

Martelli & Pichi-Sermolli (1951), Stone (1970a,b, 1975) and Huynh (1979) questioned the conspecificity of P. cruciatus, P. hermaphroditus and P. androcephalanthos. The aim of this study is to provide information on the synonymy between some pistillate...
and staminate plants. In recent years, 12 specimens of sect. Martellidendron have been collected in Madagascar (Figs 1, 2). In addition, new information has been provided from the study of herbaria specimens in Paris (P), Florence (FI) and Antananarivo (TAN).

Both collected and herbaria specimens were examined in the light of new taxonomic characters that suggest a revision of the section in Madagascar is required.

Four species are currently known from both staminate and pistillate plants (l? cruciatus, l? andromcephalenthos, l? karuka Martelli and l? kariangensis).

One is known only from the pistillate plant (E! ma-soalensis).

In this paper, P. gallinarum Callmander is described as a new species.

The discovery of a staminate plant of E! hornei (sect. Seychellea) in the Seychelles (Callmander, 2000) revealed the importance of the subgenus for an understanding of the phylogeny of the Pandanaceae. These biogeographic and systematic implications are discussed.

METHODS

For light microscopy, parts of fresh flowers preserved in ethanol were passed through toluol, then embedded in paraffin, and microtome sectioned. The preparations obtained were stained in Astra Blue and safranin or in phloroglucinol–HCl, then mounted in Eukitt. Some hand sections were also made using the same stains.

Parts of the staminate flower were also investigated by scanning electron microscopy (Phillips XL 20). Pollen grains were acetolysed then passed through the critical point dryer and sputter-coated with 23 nm of gold. Other parts of the flower were not acetolysed.

For observation of the micromorphology of the leaves, we acetolysed some parts of leaves following the method described in Huynh (1971). We took pictures of stomata and surrounding cells with a photographic microscope (Leica diaplan, Leitz orthomat).

TAXONOMIC TREATMENTS


Tree up to 10 m tall, trunk 25 cm in diameter, prop roots rising from the middle of the trunk. Leaves flagellate, 250 cm long, 5 cm wide in the middle, 6 cm near the sheath, caniculate in the lower part then progressively attenuate in the upper quarter terminated by a long flagellum, 30 cm long; dried leaf coriaceous; leaf pleats unarmed; longitudinal and transverse veins visible on both sides, but never protruding; prickles brown; costal ribs strongly revolute when dry; marginal prickles beginning at 7 cm below the base to the apex, introrse to perpendicularly in the lower part then introrse, in the first third <1–2 mm long, 2–10 mm apart; in the mid third <1 mm long, 10–20 mm apart; in the last third to 0.5 mm long, 4–10 mm apart; midrib armed from 7.5 cm to the apex, introrse, as long as the marginal prickles from the same level; sheath 7 cm long, 7.5 cm wide at apex, 8.5 cm at base, brownish when dry, greenish in the youngest leaves; abaxial face of leaves dull, glaucous, whitish when dry. Infrutescence terminal, monosyncarpic, syncarp 40 cm long, 13 cm wide, oblong-conoid, spherical in transverse section, formed by numerous drupes; peduncle 25 cm long, 4–5 cm wide at apex, straight, trigonus; core 5–7 cm wide. Drupes connate in the mature syncarp, 35–45 mm high, 15–20 mm wide, 12–15 mm thick; pileus pyramidal-acuminoid, 8–10 mm tall; stigmas two, reniform, opposite and flat; endocarp 35–25 mm in longitudinal

length, 12–15 mm wide in the last third where it is the largest, 3–5 mm distant from the stigmas, laterally terminated by two cuspides; seed locule separated from apex to base by a fibrous mesocarp wall; superior mesocarp densely fibrous and narrow, inferior mesocarp fibrous. Staminodes arranged around the base of
Figures 3-7. *Pandanus galtinarum* sp. nov. Fig. 3. Lateral view of one drupe showing some staminodes on its base, the pileus and the two reniform opposite stigmas (black). Fig. 4. Longitudinal section through the centre of the stigmas, showing endocarp (black), seed locule (white) and stigmas (stippled). Fig. 5. Drupe in apical view. Fig. 6. Upper part of leaf flattened horizontally, showing adaxial face. Fig. 7. Basal part of leaf showing abaxial face with armed midrib.
Figures 8-12. *Pandanus karangensis*. Fig. 8. Lateral view of one drupe showing staminodes on its base, pileus and the two reniform opposite stigmas (black). Fig. 9. Longitudinal section through the centre of stigmas, showing endocarp (black), seed locule (white, in the middle of endocarp) and stigmas (stippled). Fig. 10. Drupes in apical view. Fig. 11. Upper part of leaf flattened horizontally, showing adaxial face. Fig. 12. *P. karaka*. Basal part of leaf showing abaxial face with the armed midrib.
Figures 13-16. *Pandanus karaka*. Fig. 13. Lateral view of a young drupe showing the platform on its base. Fig. 14. Longitudinal section passing by the centre of the stigmas, showing endocarp (black), seed locule (white, in the middle of endocarp) and stigmas (stippled). Fig. 15. Whole leaf (bract see text) drawing from the typo in FL! (Rollot n°3). Fig. 16. Staminate inflorescence.

each drupe; anthers mucronate with four pollen sacs.
Pistillate inflorescence with 15 bracts, the first one similar to leaves; 5-6 spikes, 20-25 cm long, 3 cm in diameter, the last one longer. Each flower holding a pistillode. Stamens on a elongated capitule, oblong-elliptic, held by a stamen column, 7-8 mm high, 1 mm wide, straight. Filament 4.5 mm long. Pistillode 6-7 mm, slightly larger than the stamen and rising from them, divided into two styles in the last upper quarter.

*Type*. Perrier 14979 (Holotype FI; Isotype P); pistillate plant; upland forest; c. 900 m altitude between Andalimenra and Mandritsara (near Ampataka); whole leaves and old drupes.

*Other material*. Perrier 10996 (FI); Manongarivo massif, near Mt Antsatrotra; drupes and whole leaves. *Perrier 11010* (P & FI); staminate plant; forest of Analamazaotra; 800 m; near a pond; inflorescence and
Figures 17-20. *Pandanus karuka*. Fig. 17. Partial mid-level transection of a mature anther (hatched: remnant of intralocular partitions, fine hatched: vascular bundle). Fig. 18. Mid-transverse section in a staminode filament (lignified cells stippled: vascular bundle with minute cells in centre). Fig. 19. Transverse sections in the unforked part of a pistillode at upper level (black: xylem of the vascular bundles, hatched: phloem, stippled: parenchyma). Fig. 20. Transverse sections in the forked part showing one style (hatchings as Fig. 19).

bracts. *Guillaumet* 4281 (P); Forest of Lakato (Centre-East); 1000 m. alt.; vii.1973; leaves apex and young core with young drupes. *Guillaumet* 3851 (P); Manantenina Forest Dauphin Forest on sand; 6.vii.1971; leaves apex and lower part without drupes. *Guillaumet* 4271 (P); forest of Lakato; whole leaves with mature drupes. *Guillaumet* 2032 (FI); SW of Mananjary on road to Ambohimahasoa; rather abundant in forest; alt 800–900 m; 6.iii.1963; whole leaves and drupes. *Cremers* 2783 (P); near Beforono (Centre-East); one infrutescence with half core. *Callmander & Raveloson* M113 (NEU, TAN & G); Manankara North, near Vavary; 3.xi.1999; 13°22′51″S, 49°40′16″E; 300 m. alt.; one infrutescence and whole leaves. The vernacular name of *P. cruciatus* is ‘tsiribe’, meaning the tall *Pandanus*. Characters that distinguish *P. cruciatus* from the others include:

1. Leaf glaucous on the adaxial face (Fig. 27), long-flagellate and caniculate on the lower part, strongly revolute when dry (Fig. 24).

2. Syncarp the largest in the section (up to 40 cm), typical oblong-conoid shape, the terminal part often eaten by lemurs (Fig. 37) (Raveloson, pers. comm.), exposing the apex of the core.

3. Drupes slender, pileus pyramidal-acuminoid (Fig. 36), terminated by two large stigmas (Figs 21, 22), endocarp laterally ended by two cuspides (Fig. 23).

4. Architecture: large tree (10–15 m) with aerial roots separating from the trunk at 5–10 m, forming an entanglement of roots without a central trunk (Fig. 31).

All these characters isolate this species and make identification in the field and herbaria easy.

Huynh (1979) in his micromorphological approach of the subgenus found two micromorphological groups in Madagascar based on orientation and branching of the polar papillae of stomates, numbers of cells in the chlorenchyma and placement of fibres. On one hand, *P. hermaphroditus* and *P. cruciatus* have micromorphological similarities; on the other, nearly all species (except *P. kariangensis*) have the same stomata complex. With the type of *P. hermaphroditus* (Perrier 14979) from P, it was not possible to confirm the synonymy because the herbarium sheets contain only
Figures 21-24. *Pandanus cruciatus*. Fig. 21. Lateral view of one drupe showing some staminodes on its base, pileus and the two reniform opposite stigmas (black). Fig. 22. Drupe in apical view. Fig. 23. Longitudinal section through the centre of stigmas, showing endocarp (black), seed locule (white, in the middle of endocarp) and stigmas (stippled). Fig. 24. Middle part of leaves flattened horizontally, showing the abaxial face, the costal rib revolute when dry.
Figures 25–27. *Pandanus androcephalenthos*. Fig. 25. Terminal clump of leaves showing the hanging staminate inflorescences (arrowed) (*Callmander et al. M150*). Scale bar = 50 cm. Fig. 26. Terminal clump of leaves showing the hanging pistillate inflorescence hidden by the bracts (arrowed) (*Callmander & Wohlhauser M131*). Scale bar = 80 cm. Fig. 27. *P. cruciatus*. Clump of leaves showing the abaxial face, dull and glaucous (arrowed), compare with the adaxial face (from *Callmander & Raveloson M113*). Scale bar = 1 m.
fertile bracts that are not as similar as the sterile ones (Huynh, 1997). However, at FI we were able to observe that the first sterile bract which has a structure very close to that of leaves in Pandanaceae. This bract is caniculate in the lower part, the apex is long flagellate, and the costal ribs are strongly revolute when dry. This species has exactly the same characters as *P. cruciatus*.

When considering the name of this species, *Pandanus cruciatus* and *P. hermaphroditus* are here recognized as conspecific. Since both species were published in the same article in 1951, *P. cruciatus* is selected over *P. hermaphroditus* as the name more accurately represents the morphology of the species as Pichi-Sermolli explained (Martelli & Pichi-Sermolli, 1951): "J'ai appelé cette espèce *P. cruciatus* à cause..."
Figures 32-35. Mature syncarps and close up of drupes. Fig. 32. *P. karaka* (from Callmander & Safianinasiezy M130). Scale bar = 10 cm. Fig. 33. *P. masoalensis* (from Callmander & Raveloson M118). Scale bar = 10 cm. Fig. 34. Close up of a mature syncarp of *P. androcephalenthos* (from Callmander & Wohlhauser M131). Scale bar = 2 cm. Fig. 35. *P. androcephalenthos* (from Callmander & Wohlhauser M131). Scale bar = 10 cm.
Figures 36-40. Close-up of drupes & inflorescence. Figs 36, 37. *Pandanus cruciatus* (from Callmander & Raveloson M113), showing respectively the extra high stigmas (Fig. 36) and the core (Fig. 37). Scale bar = 2 cm. Fig. 38. Close up of drupes of *P. masoalensis*; scale bar = 2 cm. Fig. 39. Close up of drupes of *P. karaka*. Scale bar = 2 cm. Fig. 40. Staminate flower of *P. androcephalenthos* showing part of the six inflorescences hidden by the bracts. Scale bar = 30 cm.

de la croix que l’on observe sur la surface supérieur des stigmates et qui est formée par le croisement du sillon interstigmatique avec les sillons des deux stigmates.”

Figures 41-45. SEM, details of stigmas showing the different shapes and emplacement of papillae (41-43) & flowers showing the pistillode (44-45) in the centre (after taking out nearly all the stamens). Fig. 41. Pandanus kariangensis. Fig. 42. P. karaka. Fig. 43. P. androcephalenthos. Fig. 44. P. karaka. Fig. 45. P. cruciatus.

Tree to 4–6 m in height, trunk 15 cm in diameter, erect, dichotomously branched; prop roots absent. Leaves 250–350 cm long, 6 cm wide in the middle, 7 cm near the sheath, gradually attenuate in the upper part; dry leaf coriaceous in the lower part, subcoriaceous in the remaining part; leaf pleat unarmed; longitudinal and transverse veins visible on both sides, a broad M-shaped limb in the middle. Infrutescence terminal, monosyncarpic, syncarp 25 cm long, 15 cm in diameter, oblong-conical, spherical in transverse section; peduncle 38–40 cm long. Drupes connate in the mature syncarp, 3.9–4 cm high, 1.7–1.9 cm wide, 1.2–1.8 cm
thick; pileus flat, 2 mm high; stigmas two, reniform, opposite and flat; endocarp 2.4 cm long, nearly flat on the top; seed locule separated from apex to base by a fibrous mesocarp wall. Staminate inflorescence entirely enclosed by the bracts similar to leaves but wider (8 cm) at base; then becoming whitish and smaller; 15 sterile bracts then 4 fertile bracts, narrower at the apex (the last only 1 cm at base). 5–6 spikes, the last one longest (40 cm × 4 cm). Floral peduncle 22.5 cm long below the first inflorescence with a maximum...
diameter 3.5 cm; first bracts 6 cm from its base then at centimetre intervals. Pedicellate flowers; stamens disposed on a globose capitulum, held up by the stamen column, 12–15 mm long, 0.5 cm wide, flexuous. Filament 2.5 mm long. Anther lanceolate, 3 mm long, 0.6 mm wide at base. Pistillode 1.5 mm high, shorter than the stamens, divided in two styles in the upper third. Stigmas circular, thick.

Type. *Perrier 10936* (staminate), (isotypes P & FI); x.1909; Lokobe Reserve, Nosy-Be.

Other material. *Laivao NEU 2* (pistillate); (NEU & TAN); Nosy-Be, Lokobe Natural Reserve, Andranonankomba river, on beach; 13°25′13″S, 48°19′00″E; 7.v.1996. *Guillaume 2174* (TAN & P); SW of Ambanja, ravine border and slope in dense dry forest about 70 km on road to Antsiohihy 2.viii.1968; fruit. *Callmander & Wohlhauser M131*; (TAN & NEU, P); SW of Ambanja, near the road about 65 km on road to Antsiohihy; 2.xii.1999. *Callmander, Wohlhauser, Rakotonamajo & Andrianjaka M150* (SW309) (TAN, G, P, NEU); Bevavona, on road to Bemanefeky (east of Ambanja), alt. 50 m, 18.xi.2000.

The vernacular name (Sakalava language) is ‘karakantety’, meaning ‘the *Pandanus* which grows on land’.

Notes. *Pandanus androcephalenthos* was described on plants collected respectively in the north-west in Lokobe, Nosy-Be (*Perrier 10936*, staminate) and in the Manongarivo massif near the summit of Antsatratsara (*Perrier 10996*, pistillate). The type (*Perrier 10996*) at FI has one leaf and some old drupes. The leaf is long and flagellate; the abaxial face is grey, dull and the
margins are curved under the leaf blade when dry. Furthermore, the base is caniculate. The drupes are characterized by large stigmata (5 × 6 mm) that extend further than the surface of the pileus (2–3 mm), which is acuminate and pyramidal. This is not easy to see because the drupes are old and the epicarp is no longer present, but in one drupe we were able to confirm that. In Perrier 10936, complete leaves are lacking so that comparison is difficult, but we are aware that even if the bracts are long and flagellate, that character is not necessary identical for the leaves. In addition, the bracts are not caniculate in the lower part, nor revolute, and they have visible veins on both leaf surfaces.

Those two specimens definitely do not belong to the same species, but together they form the type specimen of P. androcephalenthos. However, current research has now revealed that the staminate and pistillate plants actually belong to two different species. In this paper, the staminate plant is recognized as P. androcephalenthos, and the pistillate plant is referred to as P. cruciatus. Effectively, when Pichi-Sermolli described a new species called P. cruciatus Pic. Serm. based on Perrier 14979 (Martelli & Pichi-Sermolli, 1951), he based his work on small differences essentially due to differences in the maturity of the drupes, and the drawings in Martelli & Pichi-Sermolli (1951: 25, fig. 3c–f) are based on one drupe that was not cut through the middle so that small distinctions are made in the apical form of the endocarp because he did not see the typical lateral cuspids of P. cruciatus. In contrast, in the type of P. cruciatus, the drawing in Martelli & Pichi-Sermolli (1951: 19, fig. 1f–g) was based on a drupe cut through the middle so that Pichi-Sermolli saw two cuspids on the lateral part of the endocarp.

It was decided to put the staminate plant of P. androcephalenthos in synonymy with P. nosibicus for different reasons. The problem is that the type at FI is missing the lower third of the bracts and lacks the base which is a good character for characterizing species. With the rediscovery of the staminate plant of P. androcephalenthos (Callmadder, Wohlhauser, Rakotomamoyo & Andrianjaka M150) quite close to the type locality, the problem was solved. The shape, size and texture are similar to leaves of P. nosibicus, and the plants:

1. The upper part of bracts are subcoriaceous with a broad M-shaped limb in the middle part as in the leaves of P. androcephalenthos (Fig. 40).
2. Overall shape of leaves typically 6–7 cm wide, brownish (when dried) with small prickles in the costal ribs.
3. Tree with single trunk bearing a few prop roots dichotomously branched as in P. androcephalenthos, with the external leaves typically folded and hanging (compare Figs 25, 26).
4. The micromorphology of leaves with, as in P. androcephalenthos, papillae ramified in 4–5 branches in the polar cells of stomates (Fig. 54). The typo (Laivao NEU2) of P. nosibicus holds processes (the smooth abaxial face observe by Huynh (1997) is not confirmed here).
5. Both grow in the Reserve of Lokobe, on the small island of Nosy-Be in the north-west (Fig. 1). It seems clear that only one species of the section grows on the island, an observation we made with M. O. Laivao after prospecting there between 1996 and 1999.

Perrier 10936 can be seen merely as the staminate plant of P. nosibicus. As P. nosibicus is the pistillate plant of the specimen collected by Perrier in Nosy-Be, we have to keep P. androcephalenthos as the valid name because it was described 40 years before P. nosibicus.


Tree 4–5 m tall, trunk 10–15 cm in diameter, prop roots absent; leaves ensiform, 220–230 cm long, 5.5 cm wide in the middle, 6.5 cm near the sheath; dry leaf coriaceous in the lower part, subcoriaceous in the remaining; leaf pleat unarmed; longitudinal and transverse veins visible on both sides; prickles brown; marginal prickles begin at 10–11 cm below the base, then extending to the apex, introrse, in the first third, <3–4 mm long, 4–15 mm apart; in the mid third, <2 mm long, 20 mm apart; in the upper third, <0.5 mm long, 0.5–1 mm apart; midrib armed from 11 cm to the apex, introrse, smaller than the marginal prickles at the same level, midrib prickles close to the marginal in the apex; sheath 8–9 cm long and 6.5 cm wide at apex, 7.5 cm at base, protruding from the adaxial face of the sheath; polar cells with 4–5 branched papillae on the abaxial face of mature limb. Infrutescence terminal, monosyncarpic; syncarp 20 cm long, 9 cm wide, oblong cylindrical, spherical in transverse section, composed of 150–200 drupes; peduncle 24 cm long, 2.3 cm wide at apex. 1.9 cm in the middle, straight, trigonous; drupes connate in the mature syncarp (depending on the nature of drying), 38 mm high, 17 mm wide, 16 mm thick; pileus flat, concave in centre, 4–5 mm high; stigmas two, reniform, opposite and flat; endocarp 25 mm long, 8 mm wide in the apical third where it is widest, 2 mm below the stigmas, decreasing in width from apex to base; seed locules (18 × 5 mm) separated from apex to base by a fibrous mesocarp wall; superior mesocarp densely fibrous and narrow, inferior mesocarp fibrous. Staminodes arranged around the base of each drupe; anthers mucronate with four pollen sacs, filament lignified. Pistillate inflorescence with 11 yellowish bracts, the longest 60–65 cm long, 6 cm wide; one inflorescence spike, straight, 40 cm long, 3 cm in
P. karaka; stamen column 3–5 mm long, 2–3 mm wide, 60–70 stamens, densely disposed in 3–4 whorls; filament 2 mm long; pistillode 1 mm, hidden in the middle of the stamen, divided into two styles in the first quarter; style 0.7 mm long, 0.15 mm wide, straight.

Type. Rollet n°3 (holotype FI); Ivoilina; 1909.

Other material. Callmander M070 (staminate) & M071 (pistillate); (NEU, TAN); littoral forest on sand near Maroantsetra; 15°28’24”S, 49°40’24”E; 10 m alt.; 2.xii.1998. Callmander & Safraninasyiez M126 & M130; SR of Nosy Mangabe; 15°30’21”S, 49°45’38”E; 180 m alt.; 5.xi.1999. Guillaumet 2130; (KLU); littoral forest on sand 5 km south of Maroantsetra; 23.vi.1968; (not seen this one but from the same locality). Callmander & Bemandiny M125; (NEU & TAN); near Maroantsetra; 15°27’57”S, 49°40’27”E; 5.xi.1999. St John 26556 (FI); St. Marie; n.v. “fandran balan”, Kalalan forest 75 m alt.; (this specimen is undeterminable due to the drupes being too old).

The vernacular name of P. karaka is “karaka”. We describe here both plants of P. karaka as a result of the rediscovery and the discovery respectively of the locality near Maroantsetra (Callmander & Bemandiny M070 & 71).

P. karaka Martelli was completely forgotten for over a century due to erroneous understanding of the diagnosis provided by Martelli (1913). It was assigned by Stone (1974) to sect. Dauphinensis, a placement followed by other taxonomists resulting in no further consideration of the species. Martelli wrote in (1913): “Syncarpium solitumum... stigmata 2–3 in papillium centrale, centra, plana, hypocrepica” but he did not underline the fact that the mesocarp extended throughout the endocarp between the seed locule, a discriminating and unique character of the subgenus. At FI, we were able to observe some old and young drupes and three young whole bracts. This species has never been illustrated. In fact, the specimens drawn by Stone (1970b: 113, fig. 4a–e) which he referred to P. karaka Martelli still exist. We have also collected it but we consider it to be a new species of sect. Dauphinensis that will be published later. The bracts are very similar to leaves of the other species collected (except P. cruciatus), being both long (195 cm) and wide (5.5 cm) (Fig. 15). The infrutescence, 20 cm long with drupes 3 cm high, terminated by a flat pileus (Figs 14, 39) concave at the top is undoubtedly linked with P. mosaensis and P. androcephalenthos.

The problem that faced us was to resolve whether P. karaka is conspecific with one of the two other species. Even if the staminate plants of P. karaka and P. androcephalenthos have many similarities, pistillate flowers separate them.

P. karaka differs from P. androcephalenthos although they share similarities in leaves and architecture (compare Figs 29 and 26):

1) P. karaka has a flat pileus, but is concave near the stigmas (Figs 14, 39), the syncarp is up to 9 cm wide (Fig. 35), and drupes are bright in their lateral parts. P. androcephalenthos is characterized by a wide (15 cm) oblong-cylindrical syncarp (Fig. 35) and drupes are dull at maturity.

(2) P. karaka grows in the east coast while P. androcephalenthos grows only in Nosy-Be and near Ambanja in the north-west (Fig. 1).

However the most striking differences are provided by the pistillate plant:

3) P. karaka has a straight column (Fig. 44); its stamens are wider and shorter (cf. Figs 46 and 47). The staminate column of P. androcephalenthos is flexuous (Fig. 50).

4) The styles fork a short distance from the base of the pistillode in P. karaka (Fig. 44) but fork in the middle in P. androcephalenthos (Fig. 50).

5) The shape of the stigmas is also different; reniform in P. karaka (Fig. 42) and nearly spherical in P. androcephalenthos (Fig. 43).

6) P. androcephalenthos has several inflorescence spikes (Fig. 40) while P. karaka has only one straight spike (Fig. 16).


Tree 5–6 m tall, 12 cm in diameter, trunk erect; prop roots absent; leaves 300–330 cm long, 7 cm wide in the middle, 8 cm near the sheath, gradually attenuate in the upper part; dry limb coriaceous in the lower part, subcoriaceous in the upper part; lateral falls unarmed; longitudinal and transverse veins visible on both sides, a broad M-shaped limb in the middle; infrutescence terminal, monosyncarpic, syncarp 20 cm long, 9 cm in diameter, oblong-conical, spherical in transverse section; peduncle 24 cm long. Drupes conate in the mature syncarp, 3.8 cm high, 1.7 cm wide, 1.6 cm thick; pileus dome-like, 3–4 mm high; stigmas two, reniform, opposite and flat; endocarp 2.5 cm long, nearly flat on the top; seed locule separated from apex to base by a fibrous mesocarp wall. Staminodes arranged around the base of each drupe.

Type. Laivao & Callmander M008 (holotype NEU; isotype TAN); Masoala Peninsula; 15°18’23”S, 50°04’09”E; 600 m alt.; along the pathway to Maroangady in forest. 26.ix.1996.

Other material. Laivao & Callmander M007 (NEU & TAN); 15°25’36”S, 50°00’14”; 550 m altitude. St John 26574; (FI & P); Analabe, 5 km south of Andapa 600 m
d’alt native forest with Vango; “P. discoideus” St John (n.d.). St John 26563 (F & P); Farankarainia 14 km north of Maroanstetra hillside forest; “P. flagellaris” St John (n.d.). Guillaume 4213 (P & TAN); RN of Marojejy; 12.xii.72. Callmander & Laivao M504; (TAN & NEU); RN of Marojejy near camp 2; 14°25’52"S, 49°45’41"E; 800 m alt.; 6.xi.1998. Callmander & Raveloson M118 & M120; (NEU, TAN); RN of Mananara-North, 10 km east of Vavary; 16°22’44”S, 49°39’40”E; 270 m alt.; 3.xi.1999.

When we published P. masoalensis, we took care to distinguish it from P. androcephalenthos (P. nosibicus, syn. nov.), the nearest species. A very interesting feature was discovered in a young syncarp collected by Rollot n°3. A platform was present in the basal part (Fig. 13) as occurs in the mature drupe of P. masoalensis (Laivao, Callmander & Wohlhauser, 2000: 46, figs 5, 7) but was absent in the mature drupes. This suggests that the platform disappeared with maturity, a kind of progressive lignification of tissues during infrutescence growth, and thus cannot be used as a discriminating character between species.

The fact that the platform was not present in the base of the drupes of P. androcephalenthos (P. nosibicus syn. nov) was used as an important distinction, but we know now that this is related to maturation. P. masoalensis has a syncarp similar to the one of P. karaka and P. androcephalenthos (compare Figs 32, 33 and 35).

P. masoalensis can be separated from P. androcephalenthos on micro- and macromorphological characters (Laivao et al., 2000). It is distinguished from P. karaka on the length of leaves and drupes. Furthermore, the pileus is quite different in shape; in P. karaka, it is flat and concave near the stigmas, while in P. masoalensis the pileus is dome-like and strictly convex near the stigmas (compare Laivao et al., 2000: 46, figs 5, 7 and Fig. 14).

We retain P. masoalensis at the rank of species because it was found only at higher altitudes in the mountains. A molecular approach will hopefully solve this question.


Tree <5 m tall, trunk 3.5–4 cm in diameter, dividing into several prop roots c. 2–3 m along its length; leaves flagellate, 150–220 cm long, 3–4 cm wide in the middle, 5–6 cm near the sheath, progressively attenuate in the upper quarter terminated by a long flagellum; dry leaf subcoriaceous in the lower part, flexuous above; leaf pleat unarmed; longitudinal and transverse veins visible on both sides. Infrutescence terminal, monosyncarpic, syncarp about 10 cm long, 5–7 cm in diameter, oblong-cylindrical, spherical in transverse section, formed by less than 100 drupes; peduncle total length unknown, 1 cm wide at apex, 0.5 cm at midpoint, straight; core 1.5 cm in diameter; drupes 3 cm high, 2.2 cm wide, 1.8 cm thick; pileus dome-like then nearly flat around stigmas, 4–6 mm high; stigmas two, reiform, opposite and flat, surrounded by minute protuberances on the lateral parts; endocarp 1.8–2.2 cm long, 0.9–1.1 cm wide in the apical third where it is the widest, 1–3 mm distant from the stigmas, laterally terminated by two cuspids; seed locule, 13–17 x 2–3 mm, separated from apex to base by a fibrous mesocarp wall; apex 8 mm from the base of the stigmas, 0.7 mm away from drupes bases, lateral endocarp narrowing from the apex to the base; superior mesocarp narrow; inferior mesocarp fibrous. Stamina needed arranged around the base of each drupe.

Type. Decary 5655 (holotype P); Madagascar, east, Karianga, Point of Farafangana; 5.x.1926.

Other material. Callmander & Raveloson M111 (pistillate plant); (NEU & TAN); RN of Mananara-North, 5 km east of Vavary (bekeketa); 16°22’38”S, 49°39’34”E; 300 m alt.; 3.xi.1999.

The locals call this species “akohomorika” and prop roots are used for wickerwork.

*P. kariangensis* was described by Huynh (1981). It was assigned to the new subsection *Retusi*flora due to its retuse anthers, a character rare in *Pandanus* and unique in the section (Fig. 49). This species is unique in the section due to many characters which we will discuss later. We found the staminate plant of *P. kariangensis* in Mananara-North far to the north of the sampling of Decary on which the type is based (Decary 5665). We had no difficulty in matching staminate and pistillate plants. The leaves are narrow and flexuous (rare in sect. *Martellidendron*). It is a small tree, 3–4 m high, that is similar to *P. cruciatus* because the aerial roots are produced at the mid-point of the trunk forming a tangled mass. However, it is impossible to confuse the two species because *P. cruciatus* is higher and the diameter of trunk and branches is clearly larger (compare Figs 28 and 31). The basal part of leaves is not camulate and the abaxial face is abundantly verrucate in *P. kariangensis* (Huynh, 1981), a character unique in the section (Figs 51, 53). We found the pistillate plant of this species in Mananara-North.

Unfortunately, we found only mature drupes fallen from the tree, and staminodes around the base of the drupes were too old to show whether they were mucronate or retuse. All the other species where we know both plants have the same anther apex between stamens and staminodes. In *P. cruciatus*, as for all other species, the anthers of staminodes are mucronate (Fig. 48) as are the stamens themselves (Fig. 45). Nevertheless, the discovery of the pistillate plant confirms its original aspects in that the syncarp is small,
surely the smallest of the section, and it has a unique leaf micromorphology. Discriminating characters are discussed under the new species.

To conclude, a very interesting species has been found in Manara-North which shares characters with *P. kariangensis* (relatively small infructescence) and other species (dichotomous ramification, micromorphology). Unfortunately, the stamine plant remains unknown and we have details only for the pistillate one.

6. *Pandanus gallinarum* Callmander sp. nov.

Arbor usque 2 m alta, ramis dichotomis, trunco 4–5 cm diametro, radieibus gralliformibus desinitutis; folia linearia flagellaria c. 145–155 cm longa, in medio 2.6–3 cm lata, prope vaginam 3.5 cm lata. Monosyncarpa; syncarpio 11 cm longo, 6.5 cm lato, oblongo-cylindrico, in sectione transversali circulari, circa 100 drupis composito. Drupae maturitate in syncarpio connatae, 28 mm longae, 16 mm latae, 11 mm crassae; pileo tholiformi, 8 mm alto; stigmatibus 2, reniformibus, oppositis, planis, protuberan-tibus lateralis circumnecris; endocarpio axialiter 13 mm longo, 9 mm lato in parte tertia supera ubi latissimo, apice 2 mm a basi stigma-tum distanti; loculis seminum ovoideis, 9 mm altis, 2 mm latis; mesocarpio supero angusto, copioso fibroso; mesocarpio infero fibroso. Staminido filamento antheraque composita; anthera acuminata, 4 loculis separatis praedita.

Tree <2 m tall, trunk 4–5 cm in diameter, erect, dichotomously branched; prop roots absent; leaves flagellate, 145–155 cm long, 2.6–3 cm wide in the middle, 3.5 cm near the sheath, progressively attenuate in the last upper quarter terminated by a long flagellum 10 cm long; dry leaf subcoriaceous in the lower part, flexuous above; leaf petal unarmed except for the last 20 cm; longitudinal and transverse veins visible on both sides, protruding in the adaxial face of the sheath; prickles dark brown; marginal prickles beginning at 6–7 cm above the base and extending to the apex, introrse to perpendicular in the lower part then extrorse, in the lower third <2 mm long, 2–10 mm apart, in the mid third <1 mm long, 8–20 mm apart, in the distal third <0.3 mm long, apart 4 mm; midrib armed from 7.5 cm to the apex, introrse, midrib prickles as long as the marginal prickles; sheath 6 cm long, 3.5 cm wide at apex, 4.5 cm at base, brownish when dry, greenish in the youngest leaves; abaxial face of leaves zoned, polar cells bearing papillae with 4–5 apical branches; infructescence terminal, monosyncarpio, syncarp 11 cm long, 6.5 cm in diameter, oblong cylindrical, spherical in transverse section, formed of 100 drupes; peduncle 10 cm long, 1.7 cm wide at apex, 1 cm in the middle, straight, trigonus. Drupes connate in the mature syncarp, 2.8 cm high, 1.6 cm wide, 1.1 cm thick; pileus dome-like, 8 mm high; stigmas two, reniform, opposite and flat, surrounded by a little bulge in the lateral parts; endocarp 1.3 cm long, 0.9 cm wide in the apical third, where it is the widest, 2 mm away from the stigmas; seed locule, 9 × 2 mm, separated from apex to base by a fibrous mesocarp wall, apex 5 mm from the base of the stigmas, attached 6–8 mm away from drupe base; lateral endocarp narrowing from apex to the base; superior mesocarp narrow; inferior mesocarp fibrous. Staminodes arranged around the base of each drupe.

*Type. Callmander & Raveloson M114 (bolotype NEU; isotypes G, P, TAN); RN de Mananara-Nord, 9 km east of Vavary (beke-tra); 16°22'51"S, 49°40'16"E; 300 m alt.; 3.xi.99.*

The vernacular name of this species is “tsirikese-koko”, which means literally, “the *Pandanus of the hens*”. It was thus called *P. gallinarum*.

This species is well defined. However, it differs from others by its infructescence and leaves. It has a small (11 cm) infructescence, while the minimum length in other species is 20 cm. Furthermore, the leaf is long and flagellate (Fig. 6) while the others are ensiform. *P. gallinarum* cannot be confused with *P. cruciatus* with regard to leaf, infructescence and architecture — it has flexuous, non-canicular leaves (Fig. 7) and the mature infructescence is half the length of that of *P. cruciatus*.

The new species is closest to *P. kariangensis* in dimensions of the syncarp and flexuous leaves, but can be easily distinguished by the following characters:

1. The drupes are small and narrow (Figs 3, 5) and the pileus is acuminate and terminated by stigmas. In *P. kariangensis*, the drupes are wider and the pileus is dome-like. The two stigmas are confined to a little plate at the top (Figs 8, 10).

2. The endocarp is flat on the top (Fig. 4) while in *P. kariangensis* it is terminated by two cuspid in the lateral parts (Fig. 9).

3. The leaves are long (220 cm) and flagellate (Fig. 6) but smaller (150 cm) and non-flagellate in *P. kariangensis* (Fig. 11).

4. *P. gallinarum* is a small single-stemmed tree with dichotomous branching (Fig. 30); *P. kariangensis* has many prop-roots rising from the trunk (Fig. 28).

5. The polar cells of the abaxial stomata have rami-fied papillae (like *P. karaka*, Fig. 52). Stomata belong to class V to VI following Huynh (1974); in *P. kariangensis*, the polar cells have several warts (Figs 51, 53) and the stomata belong to class II (Huynh, 1981).

Unfortunately, no stamine plants have been found. Thus only the infructescence can be used for comparisons between species. *P. gallinarum* is interesting
because it has characters shared by the two subsections, but the discovery of the staminodes flowers is essential for distinguishing species in subg. *Martellidendron*.


*P. kariangensis* is an outstanding species. Huynh (1981) was correct in creating a new subsection (*Retusiflora*) for it because it has retuse anthers, a character unique in the section and rare in *Pandanus*. The shape of stigmas and the position of the papillae at the superior face of the apex of carpellodes (Huynh, 1981) (Fig. 41) also differentiate this species from all the others in the other subsection (*Martellidendron*). Furthermore, macro- and micromorphology of leaves are also different. Subsection *Martellidendron* is characterized by pistillate plant with a one-layered endothecium in the proximal part of the connective (Huynh, 1983). We have observed the same unique layer in *P. karaka* (Fig. 17). We tried to find lignification of staminodes of *P. karaka* since this is a discriminating character between several species (Laivao et al., 2000). We found that the epidermal cells are lignified (Fig. 18) as in *P. cruciatus* (Huynh, 1981). The consistent presence of such anatomical characters show the well-founded nature of this subsection.

When fruiting, species of the section are easy to recognize, with sterile trees similar to section *Dau­phinenia* or *Rykiella*. With the former, the leaf-base typically has an auricle, while leaves of the latter are always wider (up to 16 cm). *Pandanus cruciatus* seems to be the most widespread species as it is found both on the east coast and in the north-west (Fig. 2A). In contrast, *P. kariangensis* is confined to the east coast (Fig. 2C). *P. karaka* and *P. masoalensis* are sympatric in the central east coast (Fig. 2D,E), suggesting that one species is present and the latter could be an ecotype growing at higher altitude. *P. androcephalenthos* is endemic to the north-west near Ambanja and in Nosy-Be (Fig. 2B).

**DISCUSSION**

Madagascar is famous for its variable geomorphology and climate, and for its rich endemic flora. Endemism is often found in specific regions where biotic and abiotic factors play an important role. For example, it is easy to find two endemic species (*P. biceps* (sect. *Bicipites*) and *P. pristis* (sect. *Souleyetia*)) in the massif of Ankaran to the north of Ambanja (Fig. 1), a wide, dry, eroded limestone plateau. Such specific edaphic regions are home to high endemism in different families, not exclusive to the Pandanaceae. A recent work on this region reveals endemism in different families such as Anthericaceae (*Chlorophyrum*), Taccaceae (*Taccia*) or Passifloraceae (*Adenia*) (Bardot-Vauclou, 1997). Species of section *Martellidendron* grow only in dense humid forests between 0 and 600–800 m. The Madagascan dense humid forests date back to the Tertiary, and show little change. They are home to some of the most primitive angiosperm families, viz. Chloranthaceae and Winteraceae. We know that subg. *Martellidendron* is very primitive in the genus and certainly in the family (Callmander, 2000), and its biogeography in Madagascar is not unexpected. The section is unlikely to occur on more recent geological formations or those under the influence of variable climates. In contrast, the distribution of a section showing rapid radiations is widespread throughout the island. For example, sect. *Souleyetia*, with small monocarpellate drupes and syncarps, occupies all phytogeographic regions on the island, and is the only section growing in the dry bush of the south-west. Sect. *Heterostigma*, with fleshy syncarps dispersed by rivers, also occupies all the phytogeographic regions.

In Madagascar, we often find species endemic to one forest massif. These include the high altitude *P. sparganioides* (sect. *Acanthostyla*) and *P. tsaratensis* (sect. *Souleyetia*) in the Tsaratanana massif, or *P. andringitrensis* (sect. *Acanthostyla*) in the Andringitra massif. These orophytes certainly come from differentiation of lower altitude species, and their differentiation seems to be recent (Humbert, 1928). In lower forests, between 150 and 500 m, we have collected the same species along the east coast in unexpected places. For example, *P. bipyramidus* (sect. *Stephanostigma*) was endemic to the Marojejy massif until we found it near Maroantsetra and near Fort-Dauphin, far to the south. In sect. *Martellidendron*, some species (*P. cruciatus, P. kariangensis*) seem to be widespread on the east coast, and we anticipate they will also be found far to the south. Such species come from the ancestral stock and this kind of ecology denotes a clear argument for old and declining species.

This outstanding group does not have much in common with the other sections in Madagascar. The nearest species is *P. horrei* from the Seychelles which, on the basis of morphology of staminate and pistillate plant, belongs to sect. *Seychellea* (Callmander, 2000). The potential bisexuality of flowers is rare in *Pandanus*, although pistillodes and staminodes do not
KEY TO THE SPECIES OF SUBG. **MARTELLIDENDRON**

Key to the staminate plant

1 Leaves flexuous; anthers retuse ........... *P. kariangensis*
2 Flower with one inflorescence .................. *P. karaka*
3 Flower with a pistillode higher (as high as) than the stamens ........................................... *P. cruciatus*
4 Stamens disposed on a globose capitule with a pistillode 1.5 mm high (Madagascar) ........................................... *P. androcephalenthos*
5 Stamens disposed on a plate with a pistillode 3.5 mm high (Seychelles) ........................................... *P. hornei*

Key to the pistillate plant

1 Syncarp globose with drupe more than 10 cm high; trees more than 15 m high (Seychelles) (sect. Seychelles) ....
2 Syncarp of different shape (sect. Martellidendron) ....... 2
3 Drupes with dome-like pileus ended by a plate where stigmas are confined ........................................... *P. kariangensis*
4 Syncarp oblong-conical; 40 x 13 cm .......... *P. cruciatus*
5 Pileus dome-like ........................................... *P. masoalensis*
6 Drupes dull, pileus concave in centre (east Madagascar) ........................................... *P. karaka*

**THE SUBGENUS MARTELLIDENDRON IN MADAGASCAR**

 ocor in other *Pandanus* species. We also found some vestigial pistillodes in species of the surrounding islands – including *P. borbonicus* from La Réunion or *P. palustris* in Mauritius – although it is only in subg. *Martellidendron* that it is a constant and discriminant character. So far, links with the genus *Pandanus* are uncertain. The closest species seems to be from the genus *Freycinetia*, another genus in the family that grows only in India, Indomalaysia and some Pacific Islands. In the biogeographic context of the Indian Ocean and morphogenesis of the family, this link between the two genera is very interesting. Recent confirmation of the important role of *P. hornei* in the Seychelles, the only group of islands between India and Madagascar, could be significant. Certainly, the presence of sect. *Martellidendron* in the lowland forests of the east coast of Madagascar attest to the Asiatic origin of those forests. It has to be seen as relictual even if the flora has more African affinities (Thomasson, 1997). Molecular analysis will provide more features to complete our understanding of the morphogenesis and biogeography of subgenus *Martellidendron*. It is possible, as suggested by Hotton et al. (1994), that it is more accurately treated as a genus.

**ACKNOWLEDGEMENTS**

The author would like to thank Professor Philippe Küpfner and Kim-Lang Huynh for their help, the Botanical and Zoological Park of Tsimbazaza and ANGAP (Association Nationale de Gestion des Aires Protégées) in Antananarivo for providing facilities in Madagascar, the Biosphere project in Mananara-North and the DEF (Département des Eaux et Forêts) in Maroantsetra for providing facilities in the field, Philippe Chassot and Michelle Vlimant, respectively, for the Latin translation and electronic microscopy, Jason R. Grant for linguistic corrections, Ernest Fortis and Anouk Béguin for technical support. The work was supported by the Swiss National Science Foundation (grant No. 31-45707.95).

**REFERENCES**


