



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

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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 (*P. gallinarum* Callmänder) from the Biosphere reserve of Mananara-North on the east coast is described, and *P. karaka* 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 Pandaceae is discussed in the context of Indian Ocean biogeography.

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ADDITIONAL KEY WORDS: biogeography – Indian Ocean – phytogeography – systematics – taxonomy.

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. *Seychellea* 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 endothelial 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 two-layered exine, endothelial 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 Madagascarian species. To date, only *P. androcephalanthos* Martelli is known from both staminate and pistillate plants (Martelli & Pichi-Sermolli, 1951). *P. hermaphroditus* Martelli and *P. kariangensis* Huynh are known only from staminate inflorescences, while *P. cruciatus* Pic. Serm., *P. nosibicus* Huynh and *P. masoalensis* Laivao & Callmänder 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

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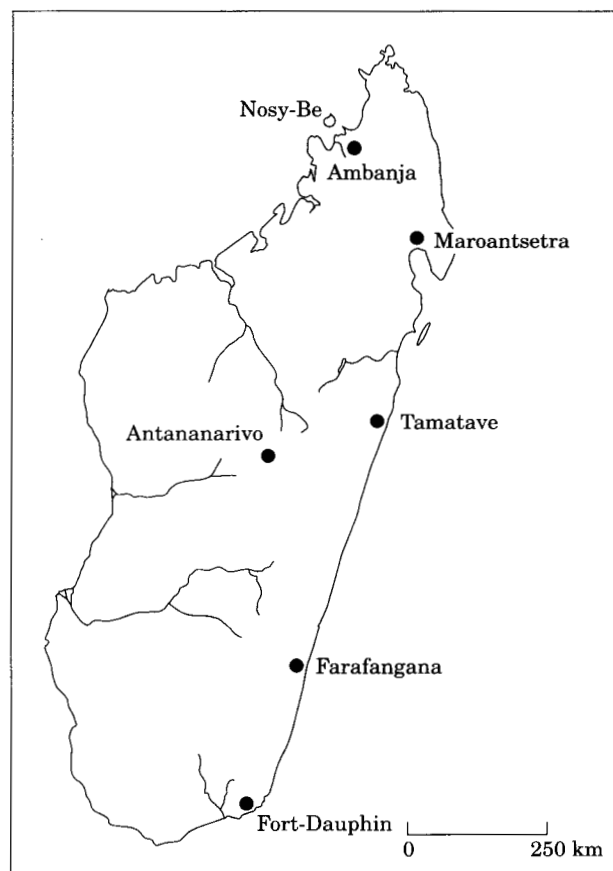


Figure 1. Map of Madagascar showing the major towns.

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 (*P. cruciatus*, *P. androcephalenthos*, *P. karaka* Martelli and *P. kariangensis*). One is known only from the pistillate plant (*P. masoalensis*). In this paper, *P. gallinarum* Callmander is described as a new species.

The discovery of a staminate plant of *P. 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 diaphan, Leitz orthomat).

TAXONOMIC TREATMENTS

1. *Pandanus cruciatus* Pic. Serm., Mém. Inst. Sci. Madagascar sér. B Biol. vég 3 (1): 33 figs 1d–1l (1951).

= *P. hermaphroditus* Martelli, Mém. Inst. Sci. Madagascar sér. B Biol. vég 3 (1): 31, figs 4a–4d. (1951), Holotype: *Perrier de la Bâthie 11010*, (P), syn. nov.

= *P. androcephalenthos* Martelli, Mém. Inst. Sci. Madagascar sér. B Biol. Vég 3 (1): 27, figs 3a–3g. (1951), Holotype: *Perrier de la Bâthie 10996*, (P), syn. nov., in part (as to the pistillate plant).

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 perpendicular 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, mono-syncarpic, 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

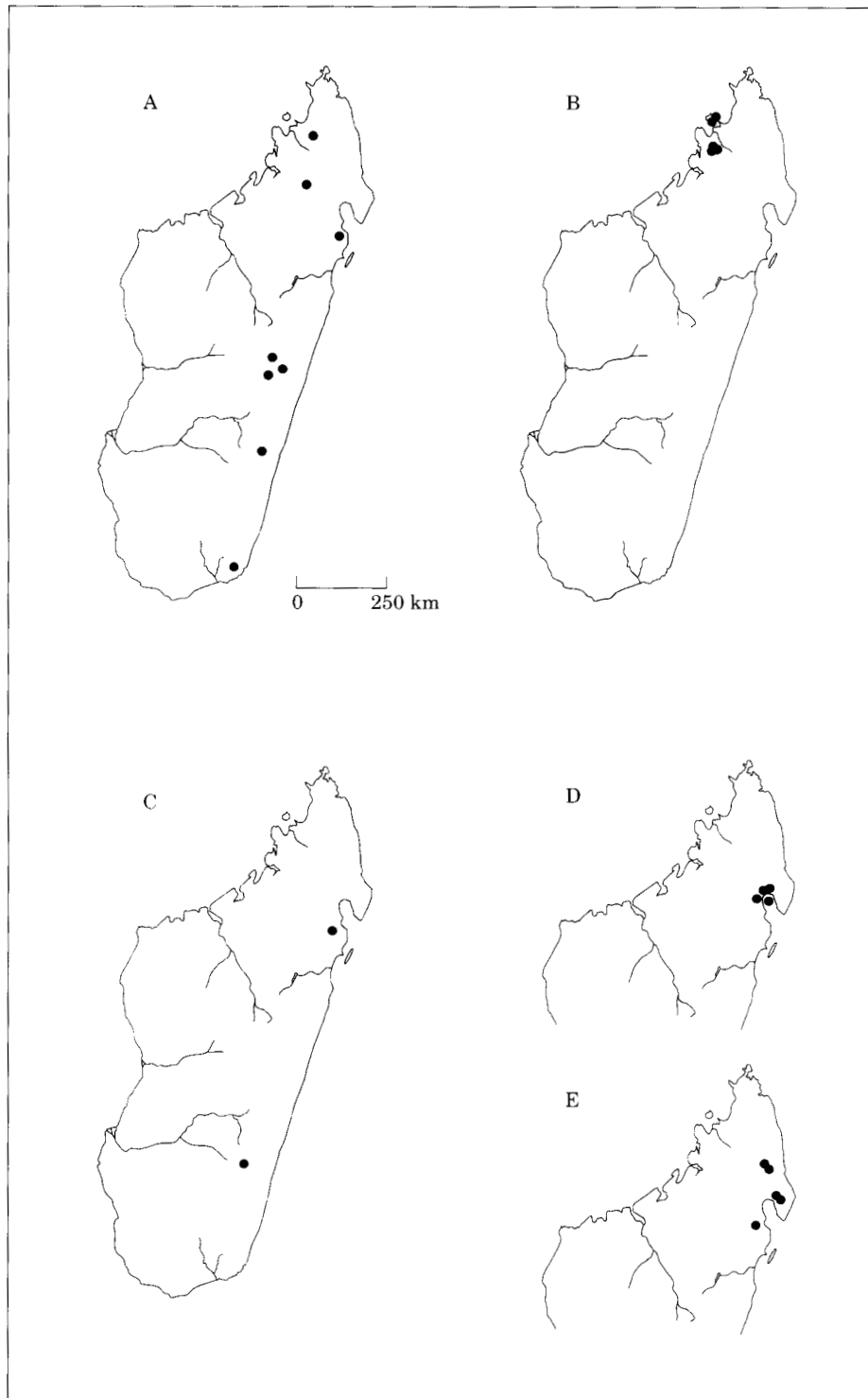
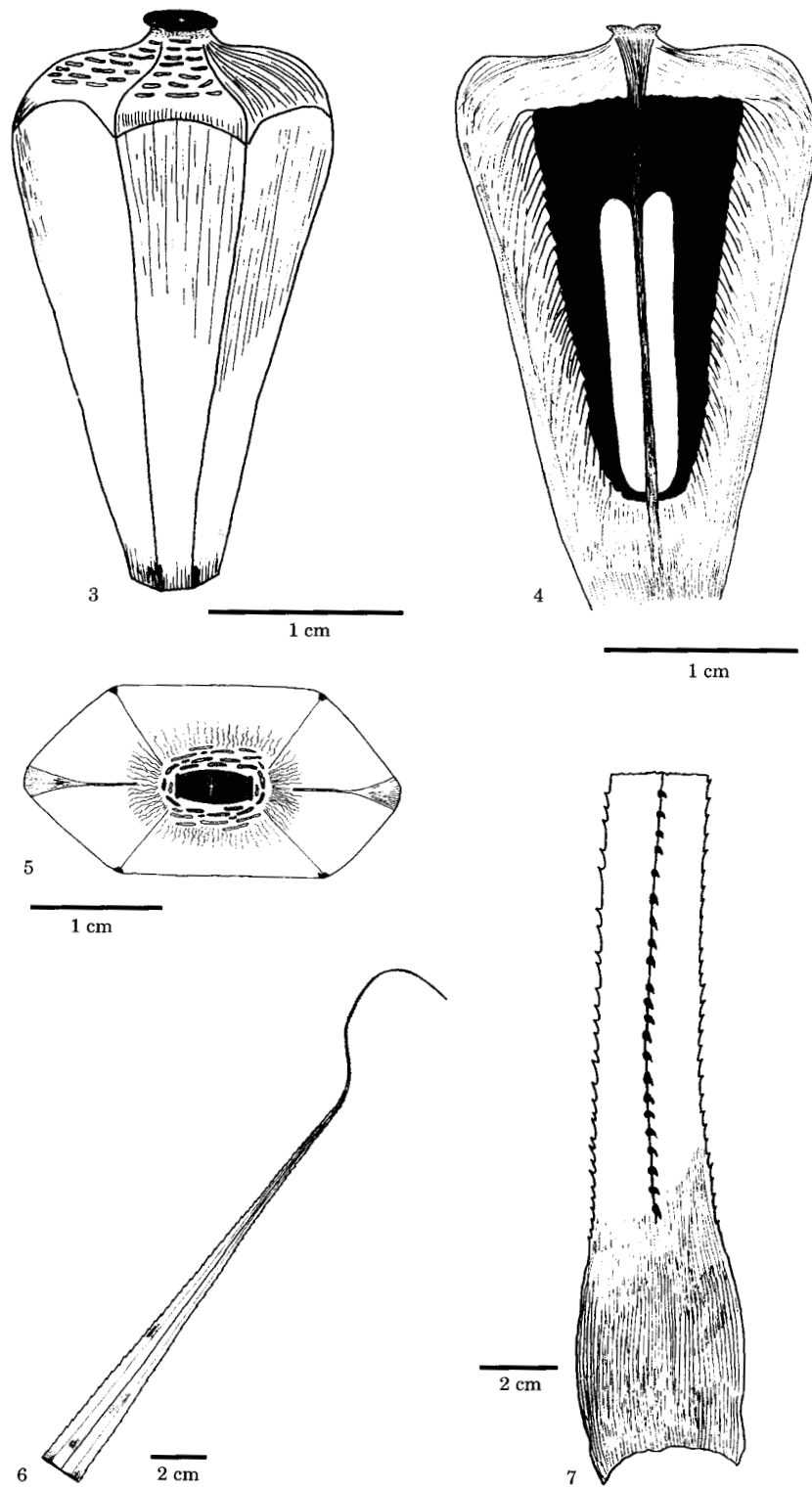


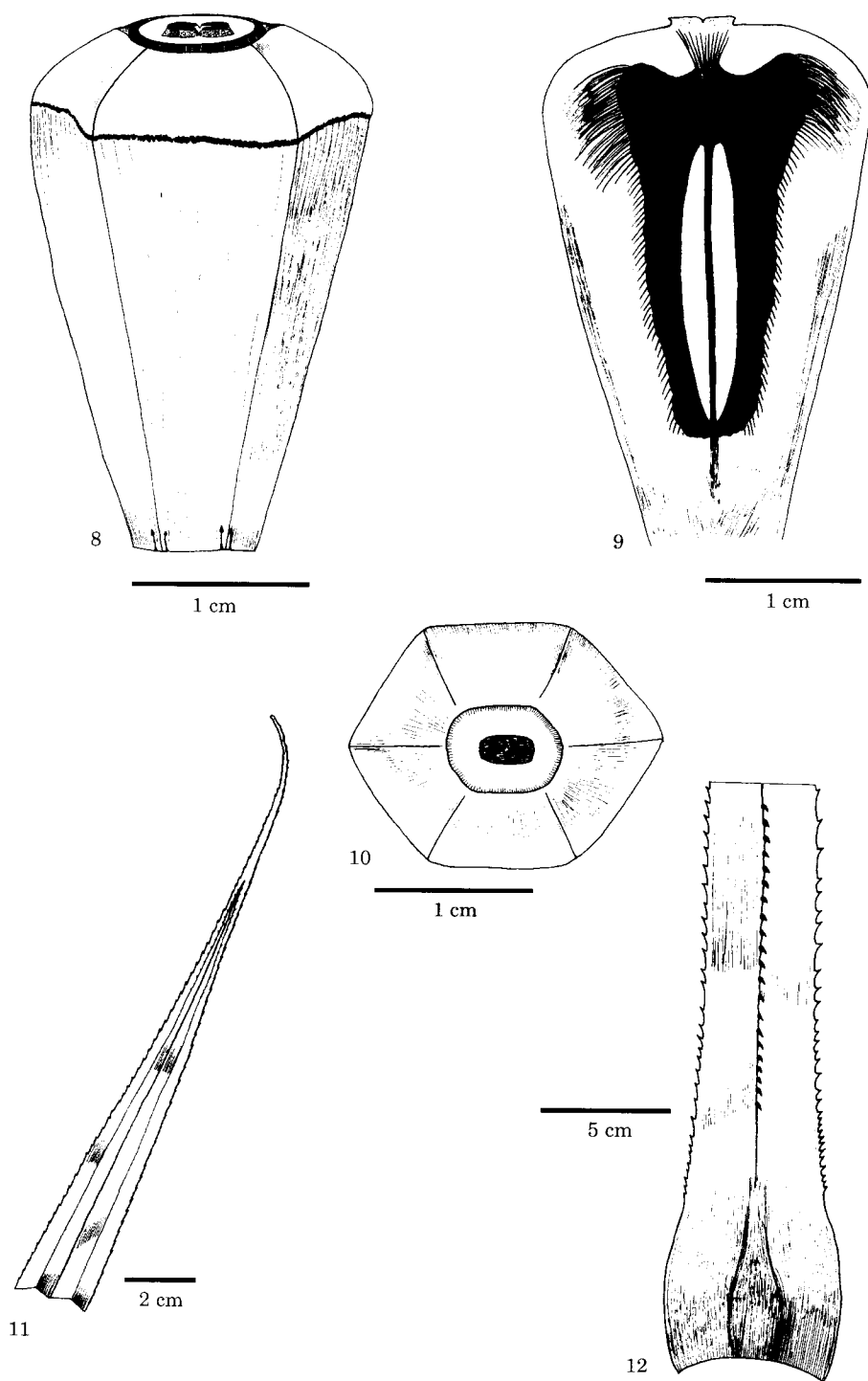
Figure 2. Map of Madagascar showing collection localities. A, *Pandanus cruciatus*, B, *P. androcephalenthos*. C, *P. kariangensis*. D, *P. karaka*. E, *P. masoalensis*.

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

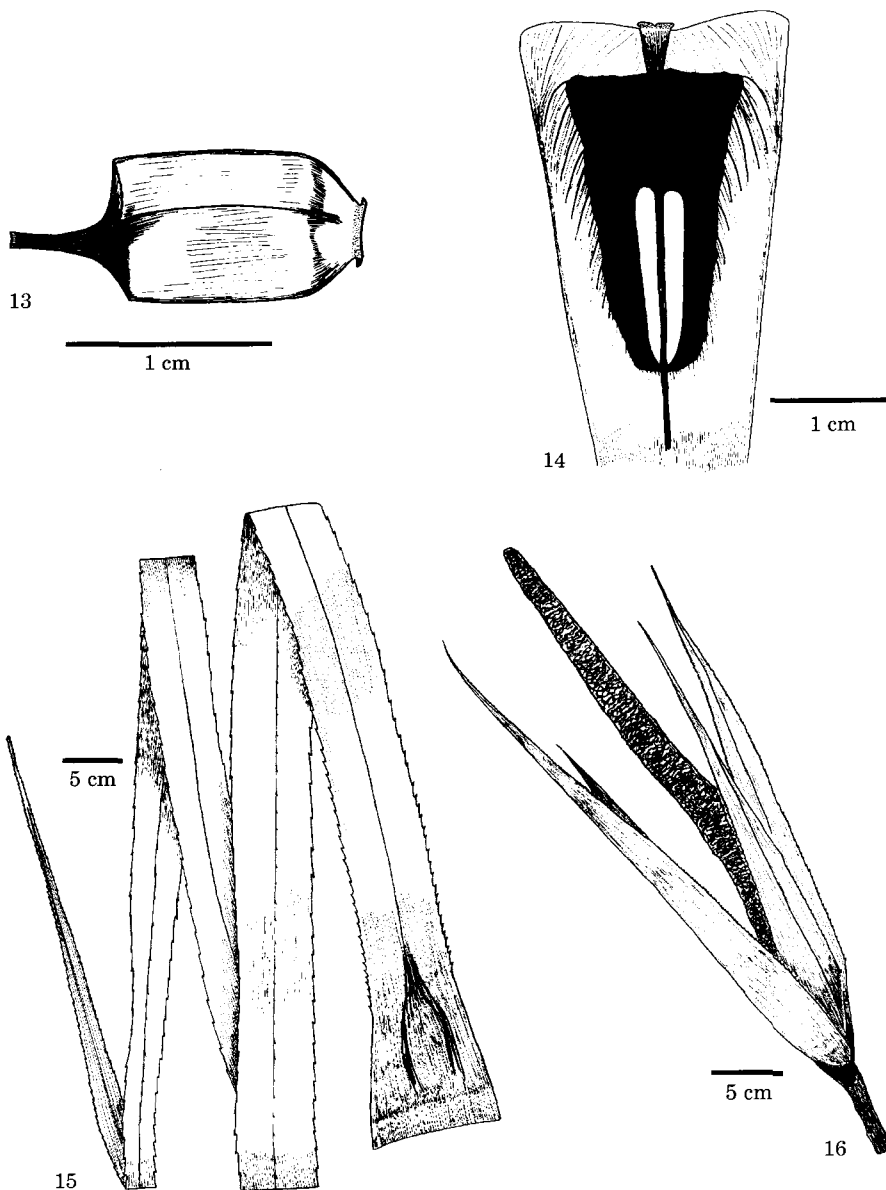
apex to base by a fibrous mesocarp wall; superior mesocarp densely fibrous and narrow, inferior mesocarp fibrous. Stamines arranged around the base of



Figures 3–7. *Pandanus gallinarum* 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 kariangensis*. 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.

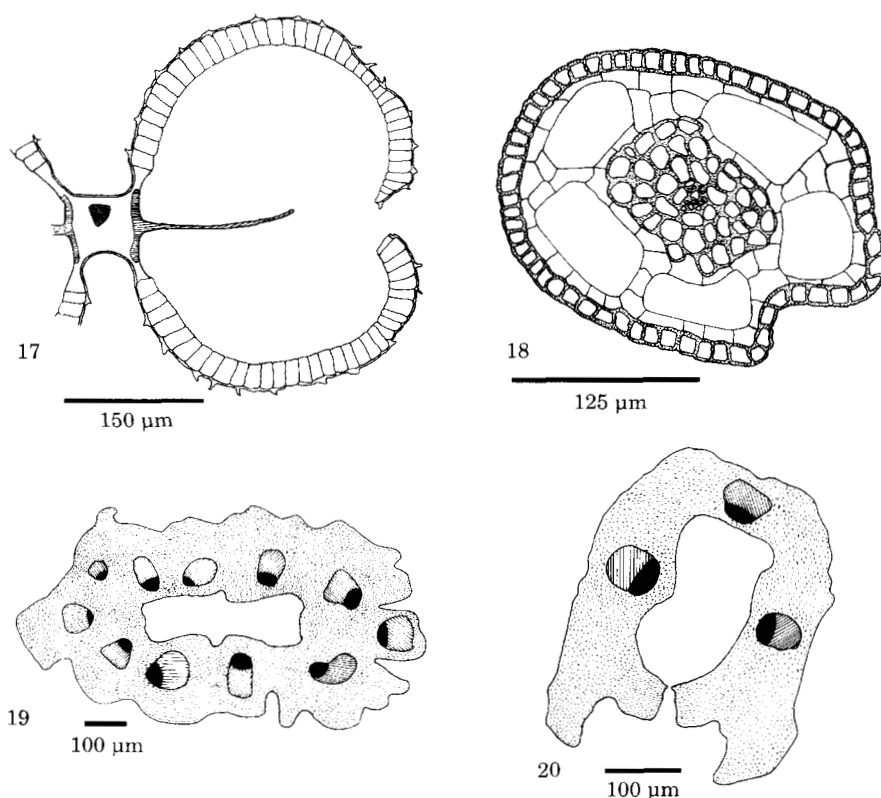


Figures 13–16. *Pandanus karaka*. Fig. 13. Lateral view of a young drupe showing the platform on its base. Fig. 14. Longitudinal section passing by the centre of the stigmas, showing endocarp (black), seed locule (white, in the middle of endocarp) and stigmas (stippled). Fig. 15. Whole leaf (bract see text) drawing from the typo in FI! (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 Andalimena 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 karaka*. 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 Fort 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 Mananjay 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 infructescence with half core. *Callmander & Raveloson M113* (NEU, TAN & G); Mananara North, near Vavary; 3.xi.1999; 13°22'51"S, 49°40'16"E; 300 m. alt; one infructescence and whole leaves. The vernacular name of *P. cruciatus* is 'tsiribe', meaning the tall *Pandanus*. Characters that distinguish *P. cruciatus* from the others include:

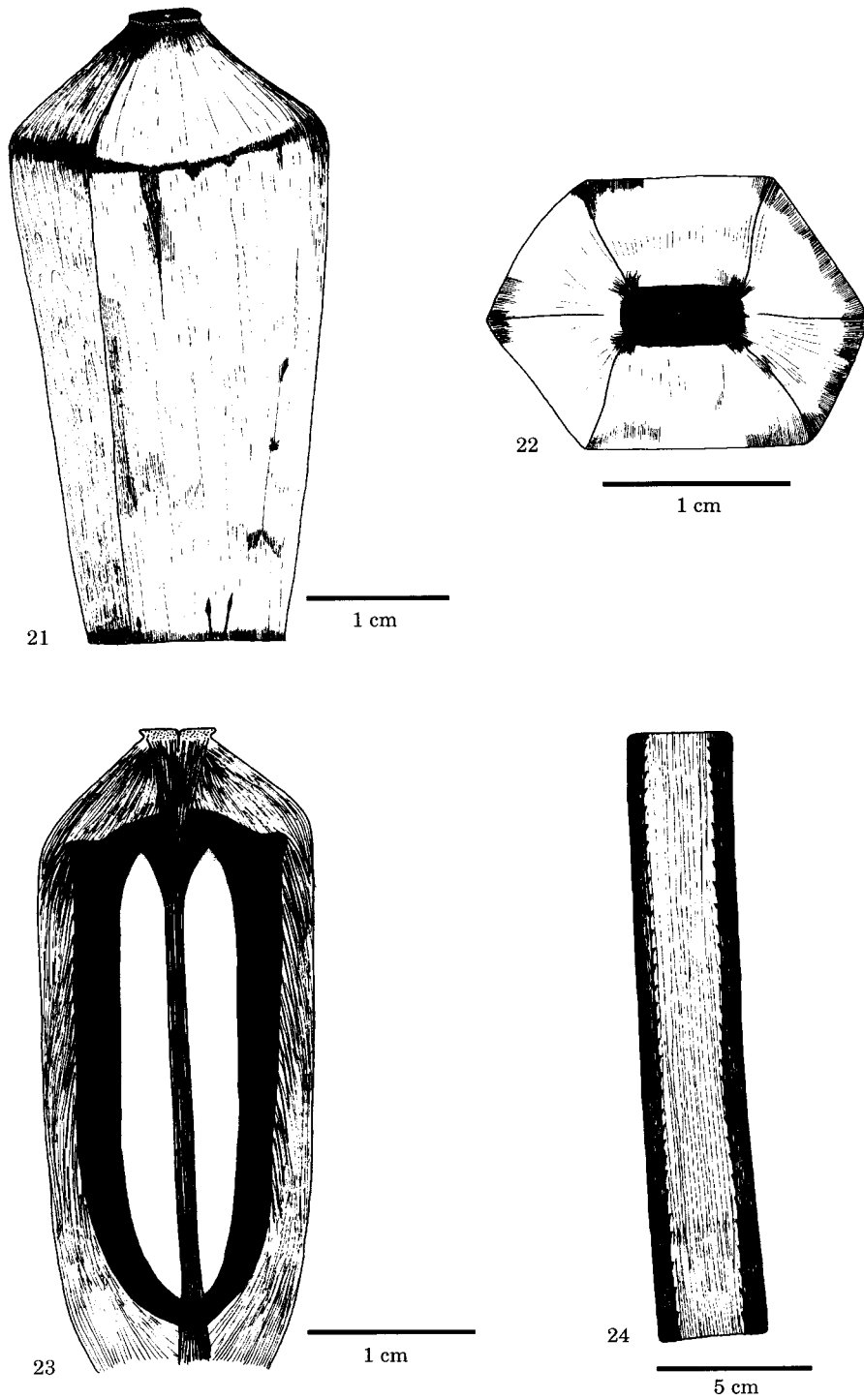
- (1) Leaf glaucous on the adaxial face (Fig. 27), long-flagellate and caniculate on the lower part, strongly revolute when dry (Fig. 24).
- (2) Syncarp the largest in the section (up to 40 cm), typical oblong-conoid shape, the terminal part

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.

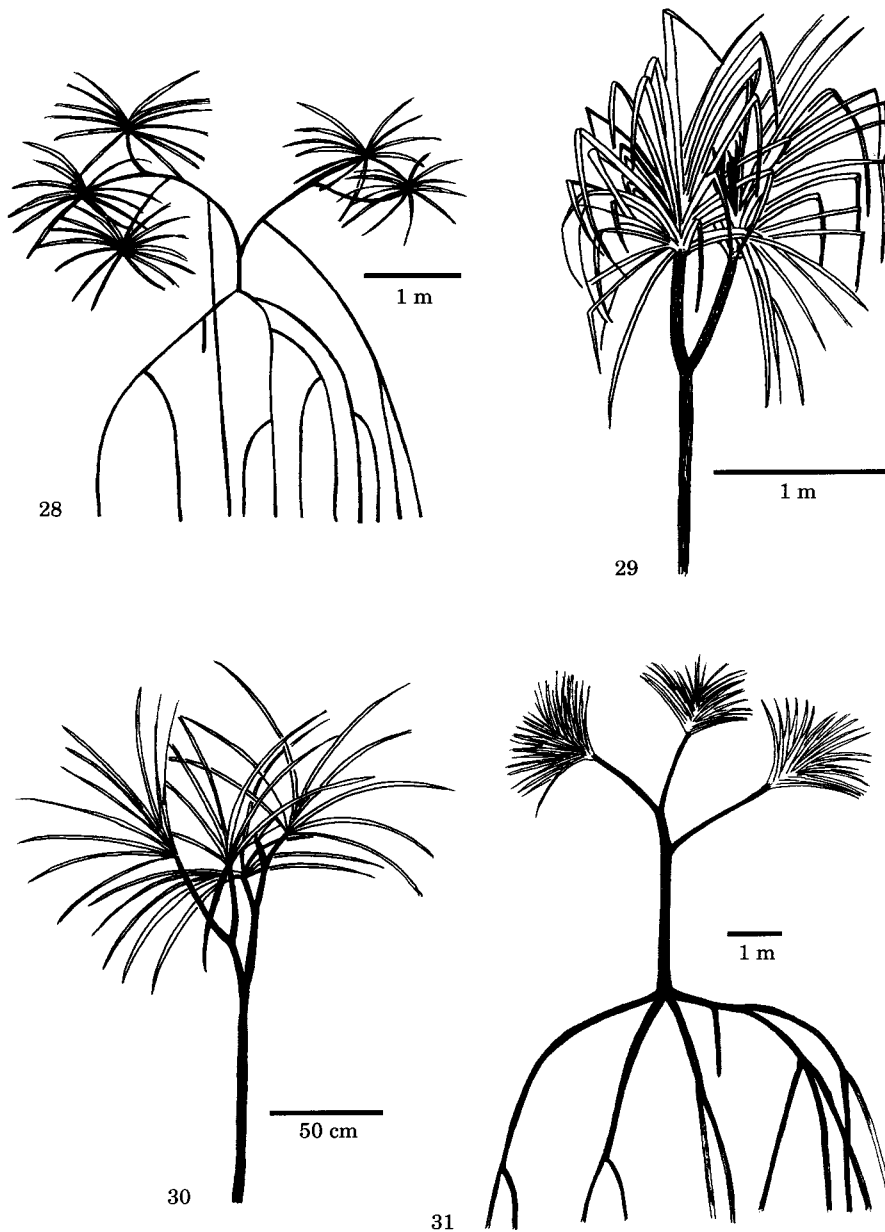
Huynh (1979) in his micromorphological approach of the subgenus found two micromorphological groups in Madagascar based on orientation and branching of the polar papillae of stomates, numbers of cells in the chlorenchyma and placement of fibres. On one hand, *P. hermaphroditus* and *P. cruciatus* have 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.



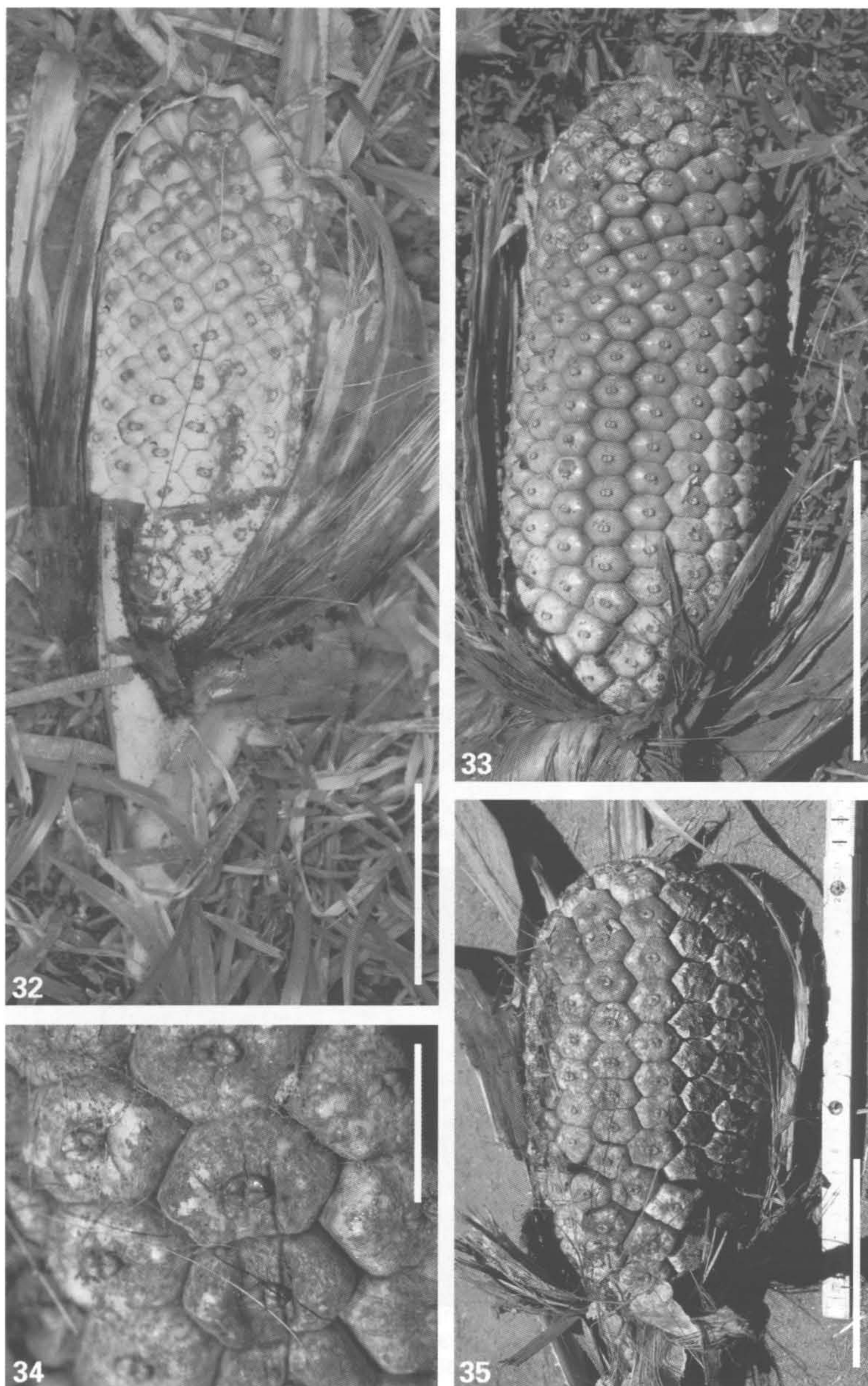
Figures 25–27. *Pandanus androcephalenthos*. Fig. 25. Terminal clump of leaves showing the hanging staminate inflorescences (arrowed) (Callmander *et al.* M150). Scale bar = 50 cm. Fig. 26. Terminal clump of leaves showing the hanging pistillate inflorescence hidden by the bracts (arrowed) (Callmander & 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.



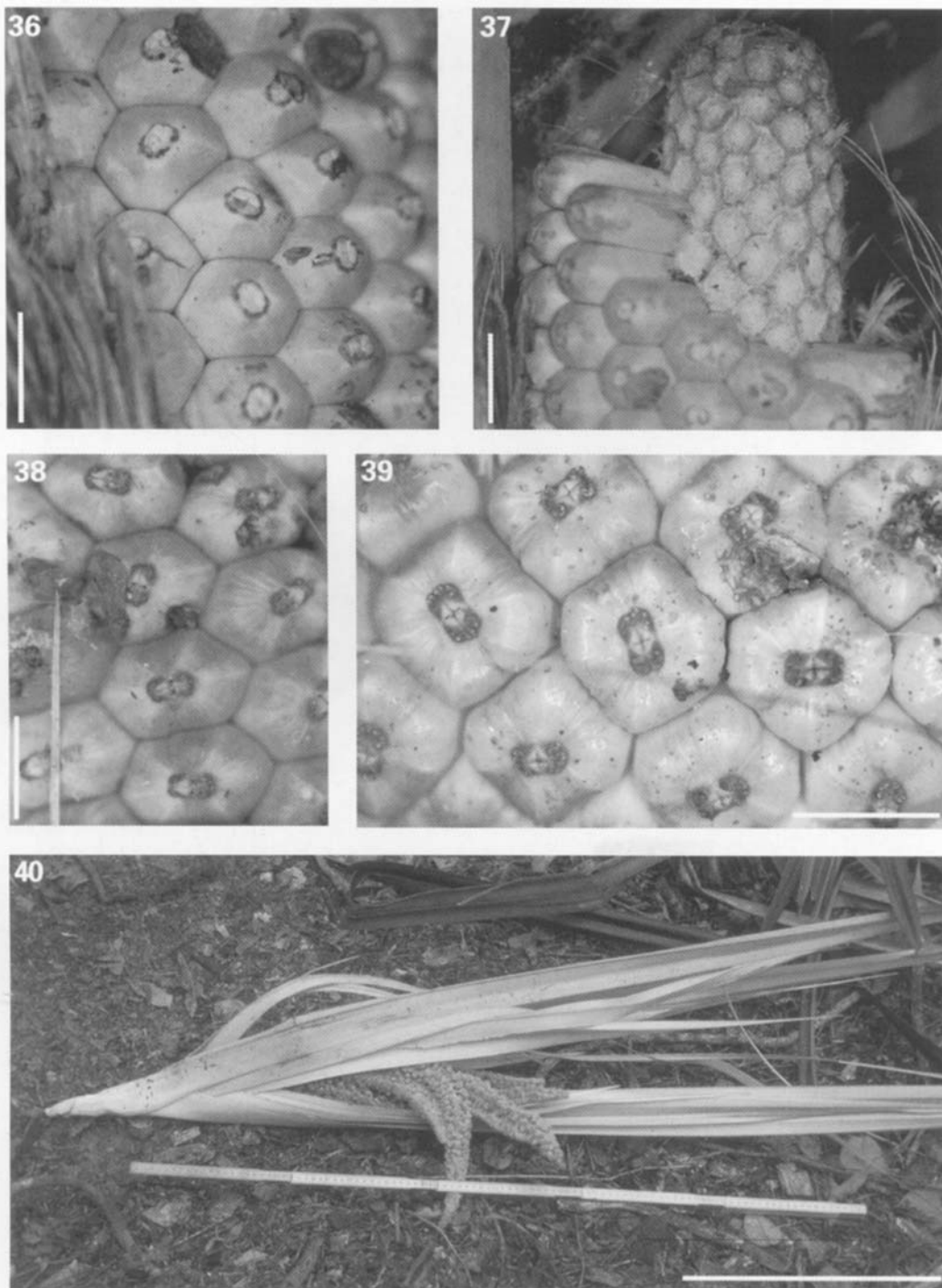
Figures 28–31. Architecture. Fig. 28. *P. kariangensis*. Fig. 29. *P. karaka*, pistillate plant showing the inflorescence (black) in the middle of a clump. Fig. 30. *P. gallinarum*. Fig. 31. *P. cruciatus*.

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



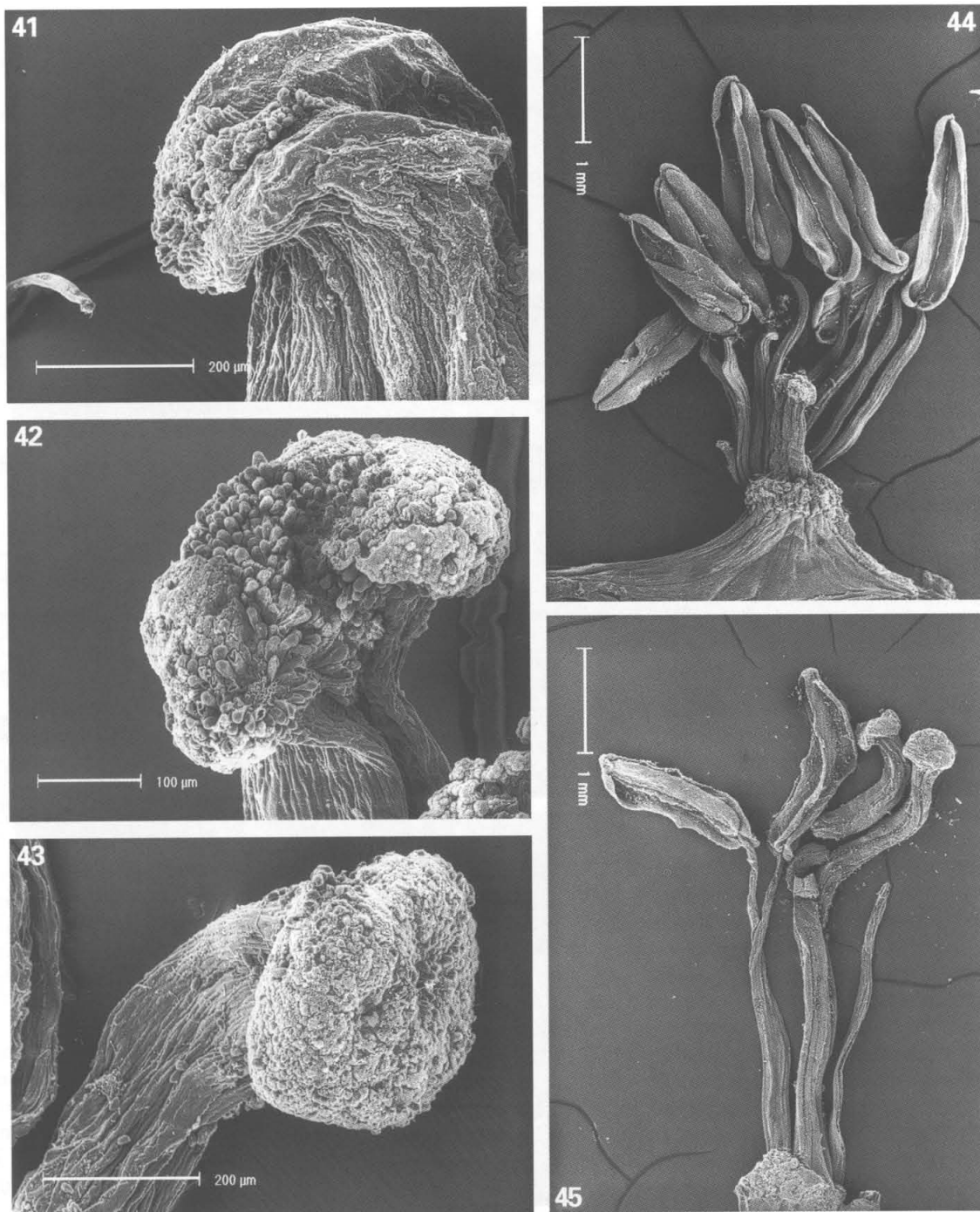
Figures 32–35. Mature syncarps and close up of drupes. Fig. 32. *P. karaka* (from Callmander & Safianinasiezy M130). Scale bar = 10 cm. Fig. 33. *P. masoalensis* (from Callmander & Raveloson M118). Scale bar = 10 cm. Fig. 34. Close up of a mature syncarp of *P. androcephalenthos* (from Callmander & Wohlhauser 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 interstigmate avec les sillons des deux stigmates."

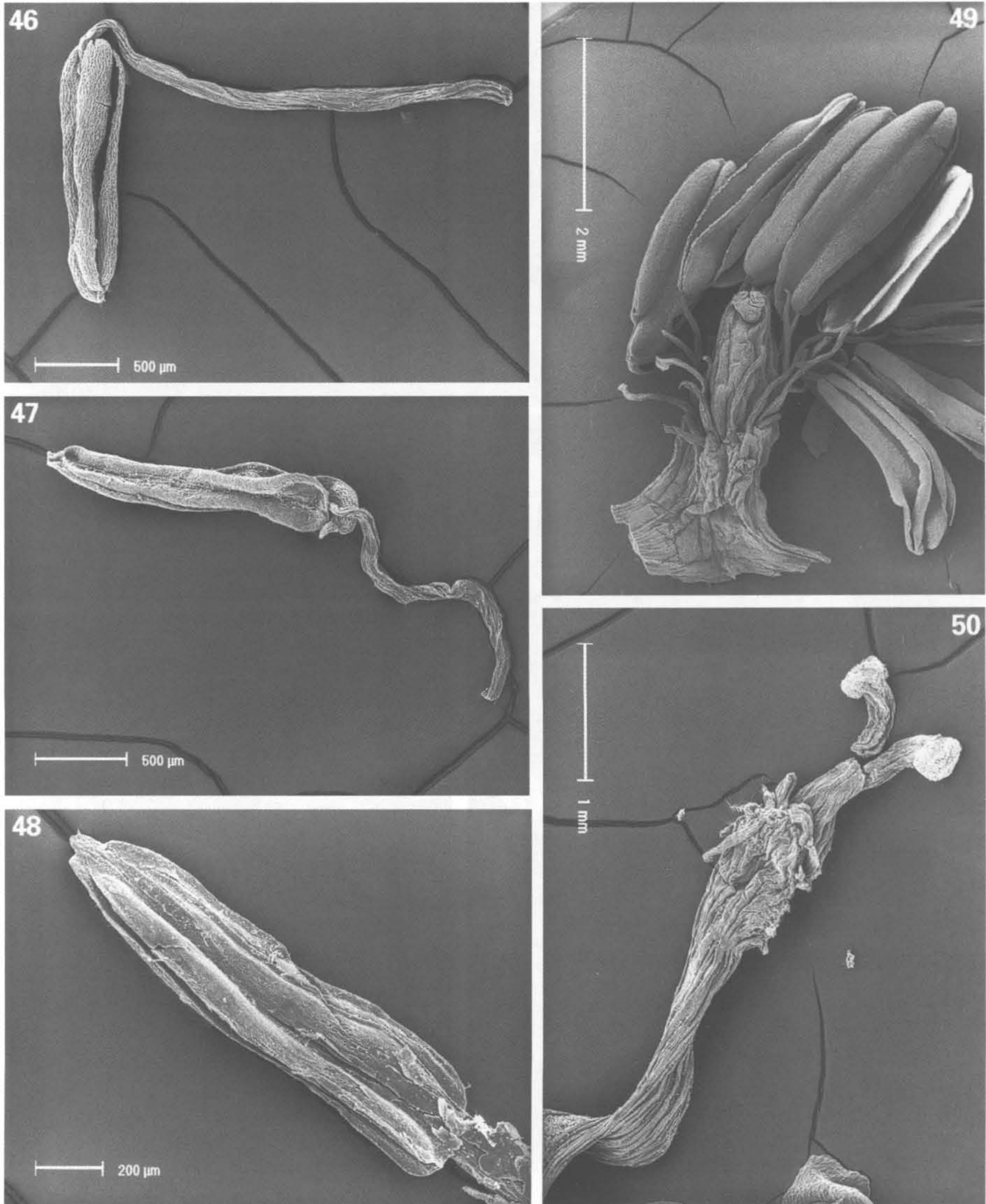
2. *Pandanus androcephalenthos* Martelli, Mém. Inst. Sci. Madagascar sér. B Biol. vég 3 (1): 27, 1951: fig. 3a–g. = *Pandanus nosibicus* Huynh, Bull. Soc. Neuch. Sci. Nat. 120: 37. 1997: figs 1–5 & 7–10, syn. nov.



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

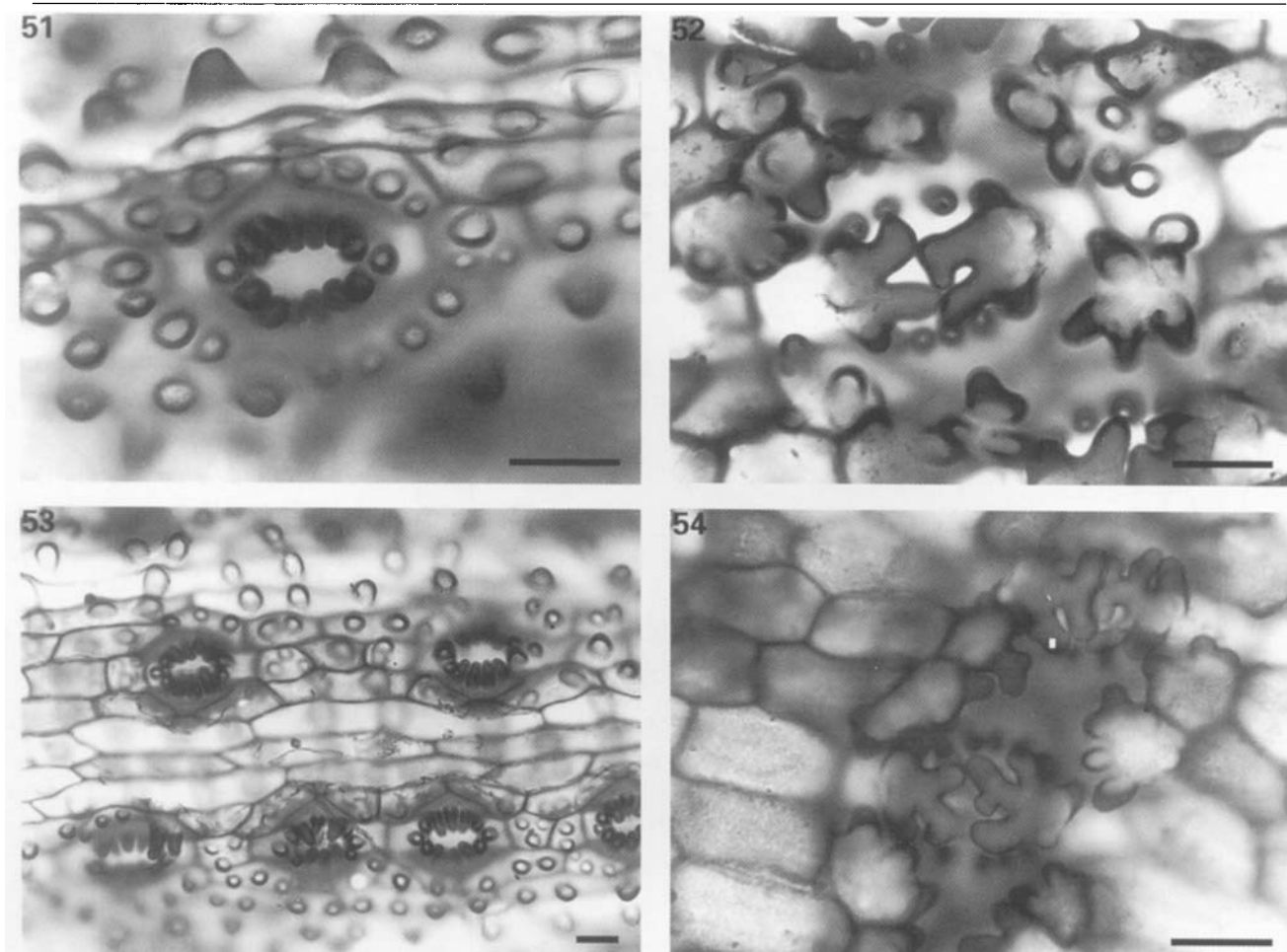
transverse veins visible on both sides, a broad M-shaped limb in the middle. Infructescence terminal, monosyncarpic, syncarp 25 cm long, 15 cm in diameter, oblong-conical, spherical in transverse section; peduncle 38–40 cm long. Drupes connate in the mature syncarp, 3.9–4 cm high, 1.7–1.9 cm wide, 1.2–1.8 cm



Figures 46–50. SEM, stamens (Figs 46, 47), staminodes (Fig. 48) and flowers showing the pistillode (Figs 49, 50) in the centre (after taking out nearly all the stamens). Fig. 46. Stamen of *Pandanus karaka*. Fig. 47. Stamen of *P. androcephalenthos*. Fig. 48. Anther of staminode of *P. cruciatus* showing the four pollen sacs and the apiculus. Fig. 49. *P. kariangensis*. Fig. 50. *P. androcephalenthos*.

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



Figures 51–54. PM (photographic microscope), stomata of abaxial face of leaf. Fig. 51. *Pandanus kariangensis*, showing the warts (see text) (*Callmander & Raveloson M111*, pistillate plant). Scale bar = 20 μ m. Fig. 52. *P. karaka*, stomata showing the ramified papillae (*Rollot n°3*). Scale bar = 15 μ m. Fig. 53. *P. kariangensis*, stomata showing the warts (see text) (*Decary 5655*). Scale bar = 20 μ m. Fig. 54. *P. androcephalenthos*, stomata showing the ramified papillae (*Callmander & Wohlhauser M131*). Scale bar = 15 μ m.

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, Andranankomba river, on beach; 13°25'13"S, 48°19'00"E; 7.v.1996. *Guillaumet 2174* (TAN & P); SW of Ambanja, ravine border and slope in dense dry forest about 70 km on road to Antsohihy 2.viii.1968; fruit. *Callmander &*

Wohlhauser M131; (TAN & NEU, P); SW of Ambanja, near the road about 65 km on road to Antsohihy; 2.xii.1999. *Callmander, Wohlhauser, Rakotomamojy & Andrianjaka M150 (SW309)* (TAN, G, P, NEU); Beavona, 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 Antsatrotra (*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 cuspid 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 cuspid 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* (*Callmander, Wohlhauser, Rakotomamojy & 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 proproots 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 type (*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*.

3. *Pandanus karaka* Martelli, Webbia 4 (2): 417, (1914).

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. Stamines 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

diameter; peduncle 15 cm long; each flower with a pistillode; 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. Rollot 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 & Safianinasiezy 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 pistillate and staminate plant not far from the type 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. *Dauphinensia*, a placement followed by other taxonomists resulting in no further consideration of the species. Martelli wrote in (1913): "Syncarpium solitarum, . . . stigmata 2–3 in papilliam centalem confortata, plana, hypocrepeca" 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. *Dauphinensia* 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. masoalensis* 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).

4. *Pandanus masoalensis* Laivao & Callmander, Bot. Helv. 110: 43, figs 2–10, (2000).

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 connate 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 (ined.). *St John 26563* (FI & P); Farankaraina 14 km north of Maroanetra hillside forest; "P. flagellaris" St John (ined.). *Guillaumet 4213* (P & TAN); RN of Marojejy; 12.xii.72. *Callmander & Laivao M054*; (TAN & NEU); NR 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); NR 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 infructescence 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.

5. *Pandanus kariangensis* Huynh, Bull. Mus. Natl. Hist. Nat. B Adansonia 3 (1): 40, figs 1–7, 16–25, 30, 31, 33–42, (1981).

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. Infructescence terminal, mono-syncarpic, 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 mid-point, 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, reniform, 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 cuspid; seed locule, 13–17 × 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. Stamminodes 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 (beketra); 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 *Retusiflora* 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 caniculate 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 infrutescence) and other species (dichotomous ramification, micromorphology). Unfortunately, the staminate plant remains unknown and we have details only for the pistillate one.

6. *Pandanus gallinarum* Callmänder sp. nov.

Arbor usque 2 m alta, ramis dichotomis, trunco 4–5 cm diametro, radicibus gralliformibus destitutis; 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, protuberantibus lateralibus circumnexus; endocarpio axialiter 13 mm longo, 9 mm lato in parte tertia supra ubi latissimo, apice 2 mm a basi stigmatum distanti; loculis seminum ovoideis, 9 mm altis, 2 mm latis; mesocarpio supero angusto, copiose fibroso; mesocarpio infero fibroso. Staminodia filamenta 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 pleat 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 antorse, 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; infrutescence terminal, monosyncarpic, 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. Callmänder & Raveloson M114 (holotype NEU; isotypes G, P, TAN); RN de Mananara-Nord, 9 km east of Vavary (bektetra); 16°22'51"S, 49°40'16"E; 300 m alt.; 3.xi.99.

The vernacular name of this species is “tsirikeakoho”, 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 infrutescence and leaves. It has a small (11 cm) infrutescence, 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, infrutescence and architecture – it has flexuous, non-canaliculate leaves (Fig. 7) and the mature infrutescence 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 acuminoid 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 cusps 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 ramified 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 staminate plants have been found. Thus only the infrutescence 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 staminate flowers is essential for distinguishing species in subg. *Martellidendron*.

Sect. *Martellidendron* Pic. Serm., Martelli & Pichi-Sermolli, Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 3 (1): 20. 1951 comprises six species of which four are known from both sexes. The type is *P. androcephalenthos* Martelli. The only species in subsection *Retusiflora*, Huynh, Bull. Mus. Natn. Hist. Nat. Paris, Sér. B, Adansonia 3 (1): 50. 1981 is *P. kariangensis* Huynh. Those in subsection *Martellidendron* (ipso facto) are *P. androcephalenthos* Martelli, *P. karaka* Martelli, *P. cruciatus* Pic. Serm. and *P. masoalensis* Laivao & Callmänder. The position of the new species *P. gallinarum* Callmänder is unclear.

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 carpelodes (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. androcephalenthos*. Furthermore, transverse sections at different levels in pistillodes (Figs 19, 20) reveal a few vascular bundles 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 *Dauphinensia* 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 Ankarana 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 (*Chlorophytum*), Taccaceae (*Tacca*) or Passifloraceae (*Adenia*) (Bardot-Vaucoulon, 1997). Species of section *Martellidendron* grow only in dense humid forests between 0 and 600–800 m. The Madagascarian 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 (Callmänder, 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. tsaratanensis* (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. hornei* from the Seychelles which, on the basis of morphology of staminate and pistillate plant, belongs to sect. *Seychellea* (Callmänder, 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*
 1 Leaves coriaceous; anthers with an apiculus 2
 2 Flower with one inflorescence *P. karaka*
 2 Flower with many inflorescence 3
 3 Flower with a pistillode higher (as high as) than the
 stamens *P. cruciatus*
 3 Flower with a pistillode hidden by the stamens 4
 4 Stamens disposed on a globose capitule with a
 pistillode 1.5 mm high (Madagascar)
 *P. androcephalenthos*
 4 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. *Seychellea*)
 *P. hornei*
 1 Syncarp of different shape (sect. *Martellidendron*) 2
 2 Syncarp up to 15 cm 3
 2 Syncarp longer than 15 cm 4
 3 Drupes with dome-like pileus ended by a plate where
 stigmas are confined *P. kariangensis*
 3 Drupes thin, compressed in syncarp and not
 terminated by a plate *P. gallinarum*
 4 Syncarp oblong-conical; 40 × 13 cm *P. cruciatus*
 4 Syncarp oblong-pyramidal; smaller 5
 5 Pileus dome-like *P. masoalensis*
 5 Pileus flat 6
 6 Lateral part of the drupes bright; north-west (Nosy-Be,
 Ambanja) *P. androcephalenthos*
 6 Drupes dull, pileus concave in centre (east
 Madagascar) *P. karaka*

occur 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 Küpfer 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).

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