

New findings on *Pandanus* sect. *Imerinenses* and sect. *Rykiella* (Pandaceae) from Madagascar

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KEY WORDS

Pandanus,
Pandaceae,
biogeography,
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ABSTRACT

Pandanus imerinensis from the east coast of Madagascar was, until recently, assigned to sect. *Rykiella* but many characters distinguish this species from other taxa found in the section (non-deciduous spiniform stigmas, habit and micromorphology). This species has been placed in the monospecific section *Imerinenses*. *Pandanus macrophyllus*, another outstanding species from the east coast is therefore the only species found in section *Rykiella*. Their taxonomic positions remain unclear. Recently, a staminate plant of *P. imerinensis* and a mature pistillate plant of *P. macrophyllus* has been found. These discoveries greatly extend our knowledge of these outstanding species. The staminate flower and pollen morphology of *P. imerinensis*, the mature pistillate plant of *P. macrophyllus* are here described for the first time. The taxonomic relationships within the genus are discussed as well as their important role in Indian Ocean biogeography. A key to the spiniform stigmas species of *Pandanus* in Madagascar is presented.

RÉSUMÉ

Nouvelles données sur le genre Pandanus sect. Imerinenses et sect. Rykiella (Pandaceae) de Madagascar.

Pandanus imerinensis de la côte est de Madagascar était, jusqu'à récemment, placé dans la section *Rykiella* mais trop de caractères isolent cette espèce des autres espèces de la section (stigmates spiniformes non-caduques, architecture et micromorphologie foliaire). Cette espèce a été placée comme type de la section monospécifique *Imerinenses* alors que *P. macrophyllus*, une autre espèce remarquable de la côte est, forme seule la section monospécifique *Rykiella*. Leurs positions taxonomiques restent peu claires. La découverte récente d'un individu mâle de *P. imerinensis* et d'une infrutescence mature de *P. macrophyllus* permet de mieux comprendre ces espèces isolées morphologiquement. La fleur mâle ainsi que la morphologie du pollen de *P. imerinensis*, et l'infrutescence mature de *P. macrophyllus* sont décrites pour la première fois. Les relations taxonomiques au sein du genre sont discutées ainsi que leur rôle important dans la biogéographie de l'Océan Indien. Une clé des espèces à stigmates spinescents des *Pandanus* de Madagascar est présentée.

MOTS CLÉS

Pandanus,
Pandaceae,
biogéographie,
phytogéographie,
taxonomie,
Madagascar,
Océan Indien.

INTRODUCTION

The paleotropical genus *Pandanus* comprises some 700 species of trees and shrubs divided in eight subgenera and fifty-five sections (STONE 1974). Madagascar is one of the major centers of diversity of the genus with nearly 100 species, nearly all of which belongs to subg. *Vinsonia* (90 spp. divided into 15 sections). However, seven species that occur along of east coast of Madagascar have a distinctive morphology that has puzzled taxonomists for the last 30 years (STONE 1970a, 1970b, 1974; HUYNH 1979a, 1979b), each of which (except one) is today placed in a small section containing one or two species: sect. *Imerinenses* (*P. imerinensis* Martelli), sect. *Phaenops* (*P. princeps* B.C. Stone, *P. longissimipedunculatus* Martelli), sect. *Lonchostigma* (*P. rollotii* Martelli), sect. *Platyphylla* (*P. platyphyllus* Martelli), sect. *Aquatiles* (*P. peyrierasii* B.C. Stone & Guillaumet) and sect. *Rykiella* (*P. macrophyllus* Martelli). These six sections are taxonomically isolated among the Malagasy species. Many characters (including micromorphology of the leaves and morphology of the staminate plant) led HUYNH (1977, 1979a) to place all of them in the African subgenus *Vinsonia* rather than the southeast Indian, and Malaysian subgenus *Rykia* despite the fact that they have many shared characters with the latter group (e.g. ecology, spiniform stigmas, monolocular drupes).

Between 1996 and 2001, we collected more than 150 specimens of *Pandanus* in preparation for a taxonomic revision of the genus in Madagascar, including a staminate plant of *P. imerinensis* and a mature pistillate infructescence of *P. macrophyllus*, neither of which have ever been described before. These discoveries open up new perspectives for understanding the affinities between Asian and the Malagasy species and for resolving the affinities of some of the small sections. After a discussion of the taxonomic importance of these discoveries, a biogeographical analysis of these small sections is provided. A key to the species is also provided.

METHODS

Parts of the staminate flower were investigated by scanning electron microscopy. Pollen grains were

acetolysed then passed through a critical point dryer and sputter-coated with 23 µm of gold. The other parts of the flower were not acetolysed. A Philipps XL 20 was used for scanning electron microscopy.

For observation of leaf micromorphology, we acetolysed some parts of leaves following the method described in HUYNH (1971).

The herbarium specimens examined are those from our collections (see list under the species) and in the herbaria of Florence (FI), Antananarivo (TAN) and Paris (P).

TAXONOMY

Pandanus imerinensis Martelli

Webbia 2: 436, pl. 19 (figs. 16-18) (1907); Martelli & Pichi-Sermolli, Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 3: 166 (1951); Stone, Webbia 24: 588 (1970); Guillaumet, Webbia 28: 503, 506, fig. 4 (1), pl. 43 (2), pl. 48 (2) (1973); Stone, Bot. Jahrb. Syst. 94: 511 (1974). — Type: *Rollot 10*, Madagascar, Tamatave province, 1906 (holo-, FI!).

Large trees 7-10 m tall, 16-20 cm in diameter at base, robust, straight, with 4-6 branches each ending in a clump of scythe-shaped leaves, prop roots forming a cone with the apex at 1-1.5 m above ground. Leaves caniculate, coriaceous, 75-80 cm (120-130 cm in pistillate plants) in length, 5 (-8) cm wide near the base, 3.5-4(-6) cm in the middle, with two auricles at base 6(-15) × 0.8 (-1) cm, acuminate, not flagellate; marginal prickles beginning 6(-15) cm from the base, 4(-6) mm long, up to 7(-10) mm apart, midrib armed with small prickles at 13(-20) cm from the base to the apex; when dried, abaxial face light brown, adaxial face dark brown, easily split apart at the midrib when flattened. Terminal inflorescence pendant in the middle of the clump of leaves; peduncle 73 cm long, 1.5 cm in diameter, spherical, hispid, bearing 11 bracts, the first three sterile; internodes 1-4 cm (7 cm between the first and the second); first bract born 23 cm from the base, all bracts lanceolate; the lowermost is 35 cm long, 4-5 cm wide in the middle; the midrib and the costal rib armed from 12 cm to the base with little prickles (0.3-0.5 mm long) up to 1-2 mm apart; bracts flexuous in the

lower 1/4, then subcoriaceous, abortive in the last three inflorescences; subtending 14 inflorescence spikes (up to 17 cm long, 3 cm wide); flowers arranged densely in each spike of the inflorescence; 3-20 stamens per flower (the filaments is often fused); anthers 1.5×0.3 cm, mucronate, arranged at the apex of the filament; the filament is 6-10 mm long, 0.7-1 mm wide, often fused (up to 5-8 mm wide). Pollen grains obovoid to spherical, $20 \mu\text{m}$ long, spinulose, with an apical aperture.

MATERIAL STUDIED. — MADAGASCAR: *Callmander & Bemandiny M122* (pistillate plant), *Callmander & Bemandiny M123* (staminate plant), Maroantsetra, Nantoroka road, $15^{\circ}27'57''\text{S}$, $49^{\circ}40'31''\text{E}$, 5 Nov. 1999 (G, NEU, P, TAN); *Perrier de la Bâthie 13290*, Tampina south of Tamatave, Nov. 1929 (FI, P); *Perrier de la Bâthie 14096*, near Vatomandry, Nov. 1921 (FI, P); *Rollot 10*, Tamatave province, 1906, type (FI).

NOTES. — This species occurs along the east coast of Madagascar, in swamps, often in secondary littoral forest from elevation 0-30 m (Fig. 1). Its vernacular name is Bobaka in the Betsimisaraka language.

Pandanus imerinensis is a remarkable species. It was first placed by STONE (1970a) in *Pandanus* sect. *Rykiella* (subg. *Rykia*) because of its comparable spiniform style (Fig. 3B), but later he assigned it to section *Lonchostigma* along with *P. rollotii* and *P. peyrierasii* (STONE 1974), although he indicated that it was «... placed here with much doubt, for although the styles are comparable, other characters are greatly different; especially the multi-cephalic inflorescence on its long, hispid peduncle.» (cf. Figs. 3A, 3D). HUYNH (1979a) then based his new monotypic sect. *Imerinenses* on this species, distinguishing it because of the micromorphology of leaves. With the discovery of a staminate plant, new arguments for the systematic and biogeographic position of *P. imerinensis* can be made.

The staminate flowers of *Pandanus* species are not very useful in intraspecific comparison because of low variation of its morphology, a notable exception being subg. *Martellidendron* (cf. CALLMANDER 2001). They are however useful for differentiation between sections (HUYNH 1977). *Pandanus rollotii*, whose ecology and morphology are close to members of *Pandanus* subg. *Rykia*, clearly belongs to subg. *Vinsonia*, largely

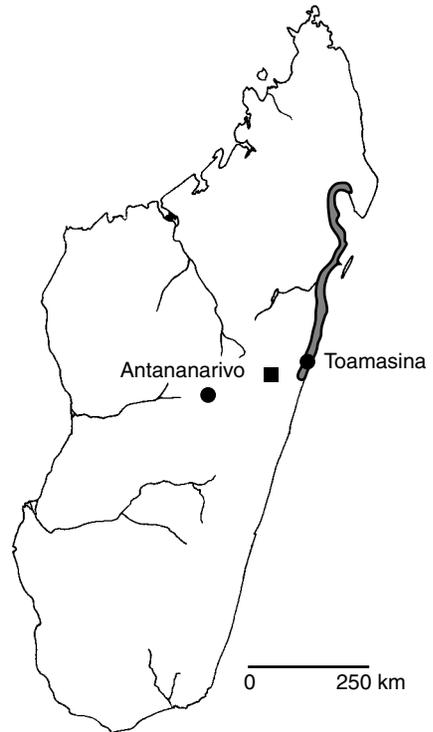


Fig. 1. — Map of Madagascar showing collection localities of members of *Pandanus* sect. *Imerinenses* (grey) and sect. *Rykiella* (black square). Major towns are indicated by a black circle.

because its staminate flowers have a candelabra-like displacement of their stamens (HUYNH 1977: 460, fig. 22) instead of the pseudo-umbel found in members of subg. *Rykia* (STONE 1974). In *Pandanus imerinensis*, the staminate flowers also have a candelabra-like stamen disposition (Fig. 6E), but this is a result of secondary ramification of the stamen columns, whereas in *Pandanus* subg. *Rykia* the stamen column is never twice ramified (This is especially evident on the type of *P. ceylanicus* (MARTELLI 1913: figs. 25-27, pl. 29). The anthers of *P. imerinensis* are small and mucronate (Fig. 6F), its pollen is spinulose (Fig. 6D), and its inflorescence holds many spikes (Fig. 2), all characters that are common throughout the genus. Less frequent is the hispid peduncle (Fig. 3D(a), 3D(b)), a rare character in *Pandanus* and unique to subg. *Vinsonia*. Furthermore, the micromorphology of the leaves is



Fig. 2. — *Pandanus imerinesis*, staminate inflorescence. (Callmander & Bemandiny M122). — Drawn by A. MEZOUAR.

unique among Malagasy species in having stomata with ramified papillae of class VII following HUYNH (1974) (Fig. 6C). Its diffuse architecture with little ramification (Fig. 3E) is likewise unique in Madagascar described by GUILLAUMET (1973) as icon forming to Stone's model, with lateral branches not limited in growth.

Pandanus macrophyllus Martelli

Webbia 2: 437, fig. 1 K,L (1907); Martelli & Pichi-Sermolli, Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 3: 155 (1951); Stone, Webbia 24: 588 (1970); Stone, J. Linn. Soc., Bot. 63: 107, 124 (1970); Guillaumet, Webbia 28: 506 (1973). Stone, Bot. Jahrb. Syst. 94: 511 (1974). — Type: *Rollot 11*, Madagascar, Imerina province, 1906 (holo-, FI!).

Tree < 6-7 m tall, trunk prickly, 18-25 cm in diameter, erect, dichotomously branched; prop roots few or none. Leaves flagellate, the one from the apex of the trunk as long as the lateral ones, 330-351 cm long, 15-17 cm wide in the middle, 16 cm near the sheath, terminated by a flagellum 7.5 cm long, 1-3 mm wide; dry leaves coriaceous; leaf pleat unarmed; longitudinal and transverse veins visible on both sides; prickles yellowish; marginal prickles beginning at 35 cm above the base and extending to the apex, antrorse, in the lower third < 7 mm long, 5 mm apart, in the mid third < 5 mm long, 7-10 mm apart, in the distal third < 3 mm long, apart 3 mm; midrib armed from 70 cm to the apex, midrib prickles smaller than the marginal prickles at the same height; sheath 35 cm long, 16 cm wide at apex, 20 cm at base. Infructescence terminal, plurisyncarpic, 8 syncarps, progressively smaller from the base to the apex, 9.7-10 cm long, 6.9-7.3 cm wide, ovoid, triangular-obtuse in transverse section; core 5.5-7 cm long, 2-3 cm wide; peduncle 95-105 cm long, 4 cm wide at apex, 2 cm in the middle, curved, trigonous, veins visible. Drupes wider in the apical and basal part of the syncarp, connate in the mature syncarp, 25-30 mm high, 8-13 mm wide, 3-8 mm thick, 1/7 superior free; pileus with prominent angles, dome-like, 2 mm high; stigmas (2-)3, spiniform, 8 mm high, 1.1 mm thick at base, oblique, turned towards the summit of the syncarp; endocarp 1.3 cm long, 1.5 mm wide, 1 mm away from the stigmas; seed locule oblong, 11 × 1 mm, apex 1 mm from the base of the stigmas, superior mesocarp narrow and fibrous; inferior mesocarp thick and fibrous.

MATERIAL STUDIED. — MADAGASCAR: *Callmander, Laivao & Wohlhauser M041*, 16 km from Brickaville on the RN2 to Antananarivo, 18°52'08''S, 48°59'42''E, 19 Aug. 1997 (G, NEU, TAN, P); *Rollot 11*, Imerina province, 1906, type (FI); *Stone 7848*, between Moramanga and Anosibe-Anala, North of the chute de la mort, 18 Mar. 1968 (KLU, P, BISH).

NOTES. — This species grow along the east coast of Madagascar: in lowland primary forest, often along streams, 300-600 m (Fig. 1). Its vernacular name is Vakoandrano in the Betsimisaraka language.

Pandanus macrophyllus (sect. *Rykiella*) is very interesting from the point of view of understand-

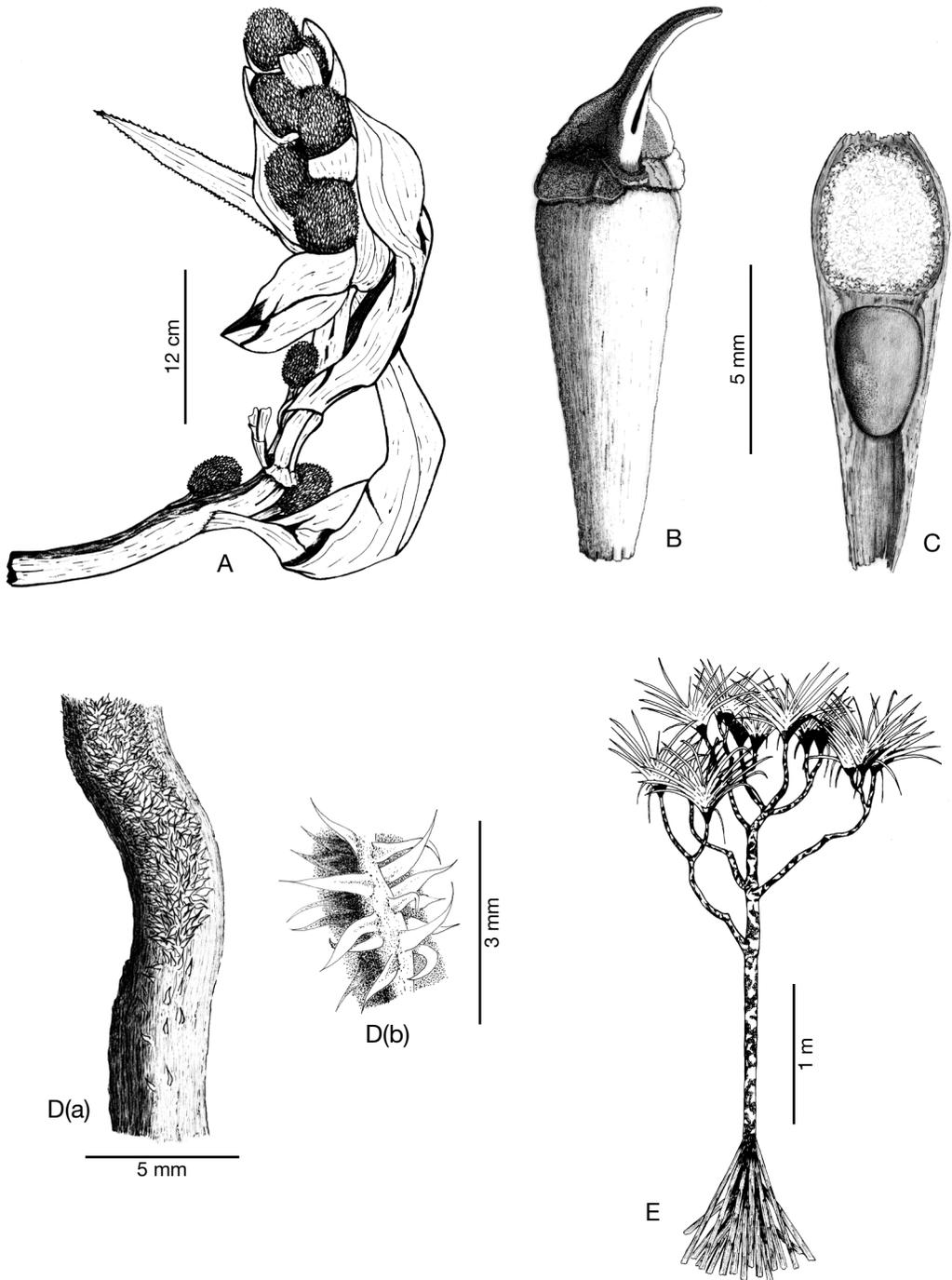


Fig. 3 — *Pandanus imerinensis*: **A**, young pistillate inflorescence; **B**, lateral view of drupe showing the stigma; **C**, longitudinal section through the centre of the stigma showing locule and fleshy upper mesocarp; **D**, peduncle of an infructescence showing its hispid surface (a) with a detail of the trichomes (b); **E**, habit showing typical diffuse architecture. (*Callmander & Bemandiny M122*). — Drawn by A. MEZOUAR.

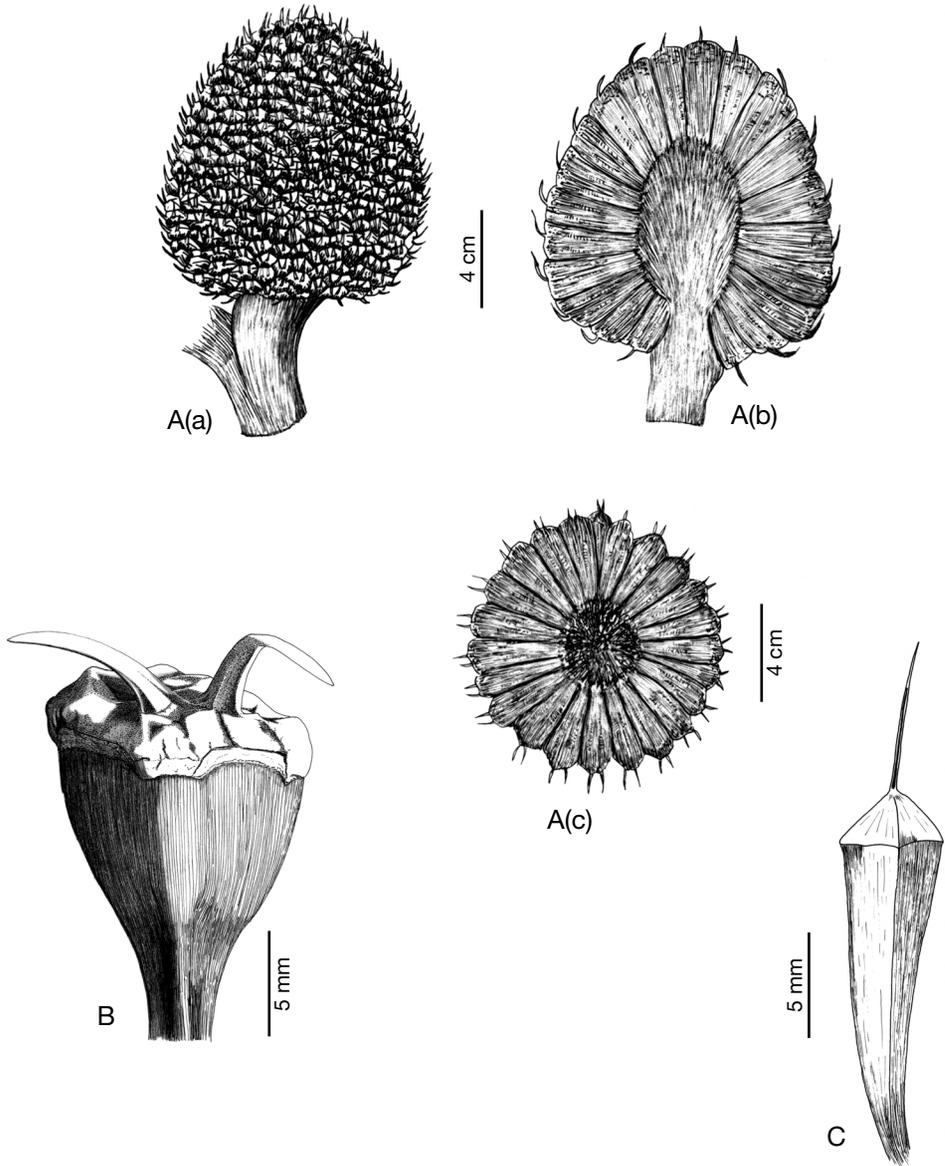


Fig. 4. — *Pandanus macrophyllus* (A,B), from specimen Callmander *et al.* M041 and *P. longissimipedunculatus* (C), redrawn after STONE (1974): **A(a-c)**, syncarp lateral view (a), longitudinal section showing the core in the middle (b) and transverse section showing spherical shape (c); **B**, lateral view of a drupe showing two spiniform stigmas; **C**, lateral view of a drupe showing long and thin spiniform stigma.

ing the origin and speciation of the Malagasy endemics.

Pandanus macrophyllus was first described by MARTELLI in 1907. It was assigned by MARTELLI & PICHI-SERMOLLI (1951) as the

type of a new section *Rykiella* by PICHI-SERMOLLI in order to point out its affinities with the sect. *Rykiea*. The type specimen (*Rollot 11*) is based on an immature syncarp, 3-4 cm long and 2.5-3.5 cm wide on a peduncle 20 cm



Fig. 5. — *Pandanus longissimipedunculatus* (A) and *P. macrophyllus* (B-D): **A**, architecture showing pendant infructescences and non-ramified habit (scale bar = 1 m); **B**, architecture showing pendant infructescence and branched habit (scale bar = 1 m); **C**, close up of a mature infructescence, from Callmänder et al. M041 (scale bar = 10 cm); **D**, young infructescence, from the type specimen Rollet 11 (scale bar = 5 cm).

long (Fig. 5D) (MARTELLI 1907), whereas mature syncarps of this species are up to 10 cm long and 7 cm wide (Fig. 4A(a)) and the peduncle is up to 100 cm long (cf. *Callmander et al. M041*). The presence of such a long peduncle is known in another Malagasy species: *P. longissimipedunculatus* Martelli (MARTELLI & PICHI-SERMOLLI 1951: 159, fig. 29a). When PICHI-SERMOLLI described *Pandanus* sect. *Rykiella*, he also included *P. longissimipedunculatus* and distinguished it on the basis of syncarp and drupe size and a peduncle length (20 cm in *P. macrophyllus* vs. 120 cm in *P. longissimipedunculatus*). HUYNH (1979a) transferred *P. longissimipedunculatus* to sect. *Phaenops* based on its micromorphology, drupes morphology and habit, an interpretation supported by the fact that *P. longissimipedunculatus* has thin, long, deciduous stigmas (Fig. 4C). Furthermore, this species is never branched (Fig. 5A) and conforms to the Corner architectural model (GUILLAUMET 1973). The micromorphology of leaves is distinctive, with a clear zonation of the stomata on the abaxial face (HUYNH 1979a) and the papilla belong to class I according to HUYNH's (1974) classification (Fig. 6A) instead of the class IIb papilla found in *P. macrophyllus*, characterized by the absence of zonation of stomata and simple papilla (Fig. 6B) (HUYNH 1974). For these reasons, HUYNH (1979a) was correct to remove *P. longissimipedunculatus* from sect. *Rykiella*. Although there is a broad affinity between *P. macrophyllus* and *P. longissimipedunculatus* — they are tall trees with thick trunks (compare Figs. 5A and 5B), large and rough leaf-crowns, and a long peduncle ending in numerous ovoid syncarps (Figs. 4A(b), 4A(c) and 5C) — similarity stops here. *Pandanus macrophyllus* is a large dichotomously branched tree (Fig. 5B), with an infrutescence characterized by a thick, straight peduncle (Fig. 5C) bearing about 8 subspherical heads, and its drupes are 2-3 celled with 2-3 non-deciduous thick stigmas (Fig. 4B), whereas *P. longissimipedunculatus* is a large monocaule tree (Fig. 5A), with an infrutescence bearing about 5-6 subspherical heads, and its drupes are one celled with one thin, long and deciduous stigmas (Fig. 4C).

DISCUSSION

Pandanus sect. *Rykiella* is important for understanding relationships among the endemic sections in Madagascar. As PICHI-SERMOLLI noted: "Je considère que *Rykiella* a une grande affinité avec *Acanthostyla*, par la structure du stigmate" (MARTELLI & PICHI-SERMOLLI 1951: 157). The stigmas are indeed rather similar in that they are thicker and stronger than those of species in the other monocarpellate sections represented in Madagascar (compare Fig. 4B and 4C) and the pileus is persistent at maturity, with prominent angles instead of being deciduous and rounded as in sect. *Phaenops*. Furthermore, the stigmas of sect. *Rykiella* are like those in *Acanthostyla* in that they have a small soft part at the base and, at maturity, the spinescent stigmas fall without the pileus. In the other spinulose sections, the pileus is deciduous at maturity and the stigmas fall with it (MARTELLI & PICHI-SERMOLLI 1951). The recent discovery of pistillate plants of *P. macrophyllus* confirms the important remarks from PICHI-SERMOLLI, and also shows that this species holds drupes with more than one stigma and nearly all drupes have 2 or 3 stigmas. This further confirms the relationship between sects. *Rykiella* and *Acanthostyla* rather than with the monocarpellate sections of the east coast (sects. *Phaenops*, *Platyphylla*, *Imerinenses*) because sect. *Acanthostyla* is the only one with spiniform stigmas with more than one-celled drupes.

The discovery of a staminate plant of a member of *Pandanus* sect. *Imerinenses* tends to confirm its systematic position in subg. *Vinsonia* rather than subg. *Rykia*. The flowers are similar to those of section *Lonchostigma* and *Aquatiles* in having a candelabra-like organization at the apex of the filament instead of an umbellate structure. Nevertheless, the five spiniform sections of eastern Madagascar coast are today considered taxonomically remote from one other. The presence of a hispid peduncle coupled with an unusual habit and micromorphology isolates *P. imerinensis*. As to *P. macrophyllus*, its macromorphology shows a link between section *Acanthostyla* and the other spiniform sections of Madagascar. It may be a relict species that combines characters from different sections (e.g. habits, polysyncarpic

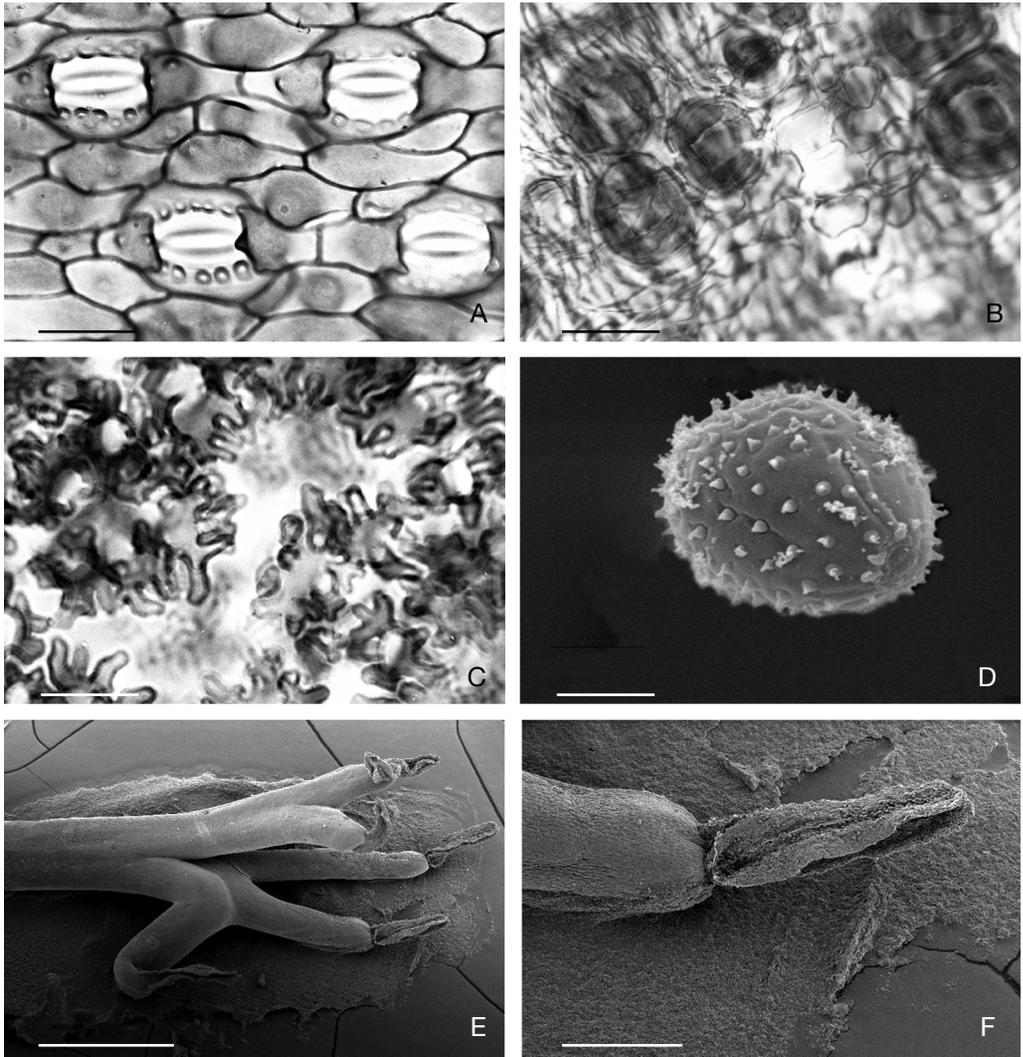


Fig. 6. — LM (light microscopy) view of stomata on abaxial leaf surface (A-C) (scale bars = 20 μ m) and SEM (scanning electron microscopy) of pollen and staminate flowers (D-F): **A**, stomata of *Pandanus longissimipedunculatus* showing papillae (Laivao et al. M034); **B**, stomata of *Pandanus macrophyllus* showing papillae (Callmander et al. M041); **C**, stomata of *Pandanus imerinensis* showing dendritic ramifications of papillae (Callmander & Bemandiny M122); **D**, spinulate pollen of *Pandanus imerinensis* (Callmander & Bemandiny M0122), scale bar = 5 μ m; **E**, staminate flower of *Pandanus imerinensis* showing the candelabra-like disposition of stamens, scale bar = 2 mm; **F**, close up of a mucronate anther, scale bar = 500 μ m (Callmander & Bemandiny M122).

infrutescences, micromorphology, ...). Each of the other monospecific sections of eastern Madagascar also has unique discriminating characters (e.g. the two lobes at the base of the stigmas of *P. platyphyllus*) but features of their staminate flower suggest a common origin, an interpretation that has been confirmed by mole-

cular phylogenetic analyses (CALLMANDER et al., in prep.).

The diversification and speciation of *Pandanus* in the lowland forest of eastern Madagascar could date back to the Tertiary. Many Malagasy species belong to genera or families that were already represented in the Cretaceous flora, and have survived

because climatic conditions have varied little over the ages (KOECHLIN 1972). The affinity between the morphologically remote endemic monospecific sections in Madagascar with *Pandanus* sect. *Rykia* from south-east India and Malaysia, coupled with their present eastern distribution suggests an ancient origin. The morphological and ecological affinities of *P. ceylanicus* Solms-Laub. from Sri Lanka with *P. rolloitii* is interesting, since Sri Lanka was part of the Gondwana continent. During the Oligocene the sea level dropped and a large part of the Chagos and Mascarene plateaux was emergent (HAG et al. 1988), which could have permitted dispersal across land or short distances of water between western Malaysia and Madagascar through India and Sri Lanka, via the "Lemurian Stepping-stone" suggested by SCHATZ (1996). The low number of species of *Pandanus* in India and Sri Lanka compared to Indo-Malaysia,

together with their morphological affinity with the Malagasy species from the east coast could be testament to this Tertiary dispersion.

The endemic *Pandanus* sect. *Acanthostyla*, with nearly 20 species growing in all phytogeographic regions of Madagascar, is a relatively diverse group compared with the other Malagasy sections with spiniform stigmas. Members of sect. *Acanthostyla* were able to cross the central N-S-running mountain range perhaps indicating a greater capacity for dispersal. Does its breeding system facilitate the process of speciation? Apparently relictual sections such as *Rykiella* may represent lineages that had no opportunity for further radiation or lineages that were once more specious and are now monospecific through extinction. Nevertheless, their presence in the lowland forest of Madagascar may indicate an ancient Gondwanan origin.

Keys to the species of *Pandanus* with spiniform stigmas in eastern Madagascar
(except species of sect. *Acanthostyla*, see HUYNH (2000) for detail species keys of this section)

PISTILLATE PLANTS

1. Stigmas deciduous at maturity; prop-roots few or none, never reaching higher than 30 cm up the trunk .. 2
- 1'. Stigmas persistent at maturity; reaching 1-1.5 m high up the trunk 5
2. Trees dichotomously branched with no leaf dimorphism; inflorescence terminal *P. macrophyllus* (sect. *Rykiella*)
- 2'. Tree never ramified or with leaf dimorphism; inflorescence lateral 3
3. Trees unbranched; leaves uniform in structure 4 (sect. *Phaenops*)
- 3'. Trees branched; leaves dimorphic (leaves of lateral branches much smaller than the crown at the top of the trunk) sect. *Acanthostyla*
4. Cephalia solitary; peduncle c. 18 cm long; style 1 cm long *P. princeps*
- 4'. Cephalia grouped in spikes peduncle long (c. 100 cm); style < 8 mm long *P. longissimopedunculatus*
5. Peduncle hispid; syncarps arranged racemosely *P. imerinensis* (sect. *Imerinenses*)
- 5'. Peduncle glabrous; syncarps solitary 6
6. Each stigma with a lateral lobe at the base; drupes < 1.5 cm long *P. platyphyllus* (sect. *Platyphylla*)
- 6'. Each stigma without lateral lobes; drupes up to 3 cm long 7
7. Fruit globose to ovoid, borne on the water surface (plants aquatic); pileus indistinct *P. peyrierasii* (sect. *Aquatiles*)
- 7'. Fruit oblong, aerial (plants growing in swamps); pileus distinct *P. rolloitii* (sect. *Lonchostigma*)

STAMINATE PLANTS

1. Peduncle hispid *P. imerinensis* (sect. *Imerinenses*)
- 1'. Peduncle glabrous 2
2. Leaves dimorphic; inflorescences born only on lateral branches sect. *Acanthostyla*
- 2'. Leaves uniform in structure; inflorescence terminal 3
3. Stamens always fused, ramified 4-7; filaments thin *P. rolloitii* (sect. *Lonchostigma*)
- 3'. Stamens sometimes free, if ramified 1-3; filaments thick *P. peyrierasii* (sect. *Aquatiles*)

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REFERENCES

- CALLMANDER M.W. 2001. — *Pandanus* subg. *Martellidendron* (Pandanaceae) part II: revision of sect. *Martellidendron* Pic. Ser. in Madagascar. *J. Linn. Soc., Bot.* 137: 353-374.
- GUILLAUMET J.-L. 1973. — Formes et développement des *Pandanus* malgaches. *Bull. Mus. Natl. Hist. Nat., B, Adansonia* 28: 495-517.
- HAQ B.U., HARDENBOL J. & VAIL P.R. 1988. — Mesozoic and Cenozoic chronostratigraphy and eustatic cycles: 71-108, in WILGUS C.K., HASTINGS B.S., POSAMENTIER H., WAGONER J.V., ROSS C.A. & StC. KENDALL C.G. (eds.), *Sea level changes: an integrated approach*. Special Publ. 42, Soc. Econ. Paleont. Mineral., Tulsa, Oklahoma.
- HUYNH K.-L. 1971. — The application of acetolysis for realising leaf cuticular membranes of *Pandanus* in taxonomic studies. *Stain Techn.* 46: 227-232.
- HUYNH K.-L. 1974. — La morphologie microscopique de la feuille et la taxonomie du genre *Pandanus* I. Aperçu général. *Bot. Jahrb. Syst.* 94: 190-256.
- HUYNH K.-L. 1977. — L'appareil mâle de quelques *Pandanus* du sous-genre *Vinsonia* (Pandanaceae) et sa signification taxonomique, phylogénique et évolutive. *Beitr. Biol. Pflanzen* 53: 447-471.
- HUYNH K.-L. 1979a. — La morphologie microscopique de la feuille et la taxonomie du genre *Pandanus* VI. 1. Partie systématique. *Bot. Jahrb. Syst.* 100: 321-371.
- HUYNH K.-L. 1979b. — La morphologie microscopique de la feuille et la taxonomie du genre *Pandanus* VI. 2. Considérations sur *P.* subg. *Vinsonia*. *Bot. Jahrb. Syst.* 100: 473-517.
- HUYNH K.-L. 2000. — The genus *Pandanus* (Pandanaceae) in Madagascar (Part 5). *Bull. Soc. Neuch. Sci. Nat.* 123: 27-35.
- KOECHLIN J. 1972. — Flora and vegetation of Madagascar: 145-199, in BATTISTINI R. & RICHARD-VINDARD G. (eds.) *Biogeography and ecology in Madagascar*. W. Junk publishers, the Hague.
- MARTELLI U. 1907. — *Pandanus*. Nuove specie. Manipulo II. *Webbia* 2: 423-439.
- MARTELLI U. 1913. — Enumerazione delle "Pandanaceae" II. *Pandanus*. *Webbia* 4: 5-105.
- MARTELLI U. & PICHI-SERMOLLI R. 1951. — Les Pandanacées récoltées par PERRIER DE LA BATHIE à Madagascar. *Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég.* 3: 1-174
- SCHATZ G.E. 1996. — Malagasy/Indo-australio-malesian phytogeographic connections: 73-83, in LOURENÇO W.R. (ed.), *Biogéographie de Madagascar*. ORSTOM, Paris.
- STONE B.C. 1970a. — New and critical species of *Pandanus* from Madagascar. *Webbia* 24: 579-618.
- STONE B.C. 1970b. — Observations of the genus *Pandanus* in Madagascar. *J. Linn. Soc., Bot.* 63: 97-131.
- STONE B.C. 1974. — Towards an improved infra-generic classification in *Pandanus* (Pandanaceae). *Bot. Jahrb. Syst.* 94: 459-540.
- STONE B.C. & GUILLAUMET J.-L. 1972. — Un nouveau *Pandanus* (Pandanacées) sub-aquatique de Madagascar. *Adansonia*, n.s. 12: 525-530.

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