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New data on the taxonomic position of *Pandanus eydouxia* (Pandanaceae), a species of the Mascarene Islands

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Abstract

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Pandanus eydouxia has been placed in subgenus *Pandanus,* then in subgenus *Vinsonia,* but data from fruit structure, anther structure and pollen morphology do not uphold either of these options. Since it cannot find a suitable position in any other known subgenus, subgenus *Eydouxia* is erected for accommodating it. Relationships of the new subgenus are also tentatively suggested.

Key words: Africa, anatomotaxonomy, anatomy, anther structure, Mascarene Islands, Mauritius, palynotaxonomy, Pandanaceae, *Pandanus, P. eydouxia, P. odoratissimus, P. spiralis, P. utilis,* pollen morphology, taxonomy.

Introduction

The genus *Pandanus* is represented in the Mascarene Islands by several peculiar species. Notably, the species with red-spined leaves (*P. utilis* Bory, *P. microcarpus* Balf. f., *P. sylvestris* Bory, etc.) (see Vaughan & Wiehe 1953) all seem to be located in these islands. *P. palustris* Thouars, an endemic species of Mauritius, one of these islands, is the only member of section *Megakeura* Stone (Stone 1974); its massive drupes on the one hand, and especially its staminate flower with staminodes forming a pistillode-like organ on the apex of the flower column (Huynh 1983a: Fig. 3A) (see also Vaughan & Wiehe 1953: Textfig. 3G) on the other hand, are two of its most noticeable features. *P. eydouxia* Balf. f., another Mauritian species, is also outstanding with its drupes formed of a high number (up to 50 or more) of flat-topped carpels; other peculiarities may be seen below.

P. eydouxia, which is examined in the present paper, was at first placed in section *Vinsonia* (Gaudich.) Warb. by Warburg (1900: 55), a section in which the stamens of the staminate flower are subumbellately arranged on the apex of the flower column (Huynh 1978). The extensive and intensive study of the genus *Pandanus* in the Mascarene Islands by Vaughan & Wiehe (1953: Textfig. 3F), however, revealed for the first time that the stamens of the staminate flower of this species were in reality racemosely arranged along the upper part of the flower column. As a result, *P. eydouxia* was removed from section

Vinsonia by St. John (1962: 414), and section *Eydouxia* St. John was described with this species as type, the other members of the new section being *P. spiralis* R. Br., *P. arnhemensis* St. John, *P. convexus* St. John and *P. integer* St. John, all from Australia. St. John (1962: 414) placed section *Eydouxia* in subgenus *Pandanus* St. John, described in a previous paper (St. John 1960: 225). The subgeneric division of *Pandanus* by St. John (1960: 225) was based on whether the drupes were all or mostly 1-celled (subgenus *Lophostigma*), or all or mostly several-celled (subgenus *Pandanus*). In several cases this separation does not correspond to taxonomic relationships between sections: for example, section *Rykia* (Vriese) Kurz and section *Multispina* Fagerl., two very closely related sections, should according to this criterium be placed, the former in subgenus *Lophostigma* for its generally 1-celled drupes, the latter in subgenus *Pandanus* because of its generally several-celled drupes. Actually, neither of these two subgenera may be considered as "natural".

The subgeneric division of *Pandanus* by Stone (1974), which seems to consider the "natural" relationships of sections in the first place, appears to reflect the taxonomic affinities better. Thus, subgenus *Pandanus* sensu Stone (1974) and especially subgenus *Acrostigma* Stone appear to be "natural", showing that solid grounds for a "natural" subgeneric division of *Pandanus* exist. Concerning section *Eydouxia,* Stone (1974: 512) retained *P. eydouxia* as the only member of the section, and removed *P. spiralis* and the other Australian species to *P.* sect. *Pandanus* subsect. *Austrokeura* Stone, in which he also included other species, most of these from Australia, the remainder from some Pacific islands (Stone 1974: 517). [This subsection was given sectional status in a further paper by Stone (1978: 238), who maintained the section in subgenus *Pandanus.*] Stone (1974: 507), in addition, placed section *Eydouxia* in subgenus *Vinsonia* (Warb.) Stone, apparently following Warburg (1900: 55), who assigned *P. eydouxia* to section *Vinsonia.*

Huynh (1979: 484) was in favour of placing section *Eydouxia* in subgenus *Pandanus* sensu Stone (1974), mainly on the basis of the racemose arrangement of the stamens of the staminate flower of *P. eydouxia* on the flower column, since in the section *Pandanus* and some other sections of this subgenus the stamens of the staminate flower have a similar arrangement. At that time, however, nothing was known about the taxonomic value of either the anther structure or the pollen morphology in the genus *Pandanus* with regard to both specific and sectional (or subsectional) relationships. Actually, there was no factual knowledge of either of these characters in this species. In the following years their taxonomic value became evident. Indeed, both characters vary from one species to another, but in all the subgenera that were studied, closely related sections or closely related species in the same sections showed the same anther structure and/or similar pollen grains: the pollen morphology in subgenera *Vinsonia* (Huynh 1980), *Martellidendron* (Huynh 1981) and *Lophostigma* (Huynh 1982); the anther structure in subgenera *Lophostigma* (Huynh 1982) and *Martellidendron* (Huynh 1983 b).

Recently, material for studying both the anther structure and the pollen morphology of *P. eydouxia* became available. As a result, the new data (described below) necessitate a reassessment of the subgeneric position of this species. The main purpose of the present paper is to show that section *Eydouxia* cannot find a suitable position either in subgenus *Vinsonia* or in subgenus *Pandanus,* or in any other known subgenus, but is the single section of a distinct subgenus.

Material and methods

For the anatomic study with light microscopy, the anthers of herbarium specimens to be studied were rehydrated, then free-hand transverse sections were made. Most of these were bleached in eau de Javelle, rinsed in water, passed through an aqueous solution of 10% acetic acid, rinsed in water again, dehydrated in ethanol, stained in a combined ethanolic solution of safranin and fast green, passed through toluol, then mounted in Canada balsam. Other sections were stained in phloroglucinol-HCl for the identification of lignified elements (tracheary elements; endothecial thickenings).

For palynological study the pollen samples to be used were acetolysed. A part of the acetolysed pollen of *P. eydouxia* was passed through absolute ethanol, then acetone, critical-point dried, mounted on stubs and subsequently scanning-electron-microscopically (SEM) examined in a Philips PSEM 500 after being sputter-coated with ca. 400 Å gold. The same method was applied to the acetolysed pollen of *P. odoratissimus* L. f., *P. spiralis* and *P. utilis,* all three studied in addition.

The other part of the acetolysed pollen of *P. eydouxia* was embedded in paraffin and microtome-sectioned at 5 µm thickness. The sections were then affixed to slides. After being observed under a light microscope, the preparations were immersed overnight in toluol for removing the cover slips and passed through absolute ethanol, after which squares of 14 × 14 mm or less and containing pollen-grain sections were excised with a diamond-marker, then passed through acetone, critical-point dried, mounted on stubs, and subsequently observed in the scanning electron microscope after being sputter-coated with ca. 400 Å gold.

The following specimens were used, all of which are staminate except *Bernardi 14869:*

P. eydouxia: Mauritius, Midlands, by side of road, 28. XI. 1966, *Lalouette MAU.12703* (MAU); Mauritius, stream bank near Bassin anglais, 16. II. 1942, *Vaughan MAU.3751* (MAU); Mauritius, Bassin anglais, 21. XII. 1946, *Wiehe MAU.3168* (MAU); Mauritius, *Bernardi 14869* (G).

P. odoratissimus: Viêtnam, 1927, *Clemens 4054* (P).

P. spiralis: Australia, sine coll. (FI).

P. utilis: Mauritius, *Michaux* s.n. (G); Mauritius, sine coll. (G); cult. Martinique, *Perrottet* s.n. (G).

Results and discussion

1. Data from anther structure

The anther of *P. eydouxia* is very narrowly oblong, up to 5 mm or more in length but not exceeding 0.7–0.8 mm in width (Fig. 1). Species with such anthers are not frequent in Africa.

The fact that *P. eydouxia* belongs neither in subgenus *Vinsonia* nor in subgenus *Pandanus* becomes evident when transverse sections of the anthers of this species are compared with those of *P. utilis,* the type species of subgenus *Vinsonia,* and with those of *P. spiralis,* one of the species in subgenus *Pandanus* with drupes most similar to that of *P. eydouxia* (drupe morphology is a main taxonomic character in *Pandanus*). In fact, a median transverse section of an anther of *P. eydouxia* generally shows the following anatomic feature (Fig. 2: disregard the asterisks), which should be taken into consideration in this comparison: the connective parenchyma around the single vascular bundle is formed of 4 or 5 cell layers and is not separated from both epidermises by cells with endothecial thickenings; in particular the absence of such cells between the parenchyma and the abaxial epidermis (i.e. the epidermis near and opposite the phloem of the vascular bundle) is very clear. In some sections (Fig. 2: note especially the asterisked cells), one or two isolated cells with endothecial thickenings may be observed in the central part of the outermost layer of the parenchyma on the abaxial side, just beneath the abaxial epidermis; and the parenchyma may be completely separated from the adaxial epidermis

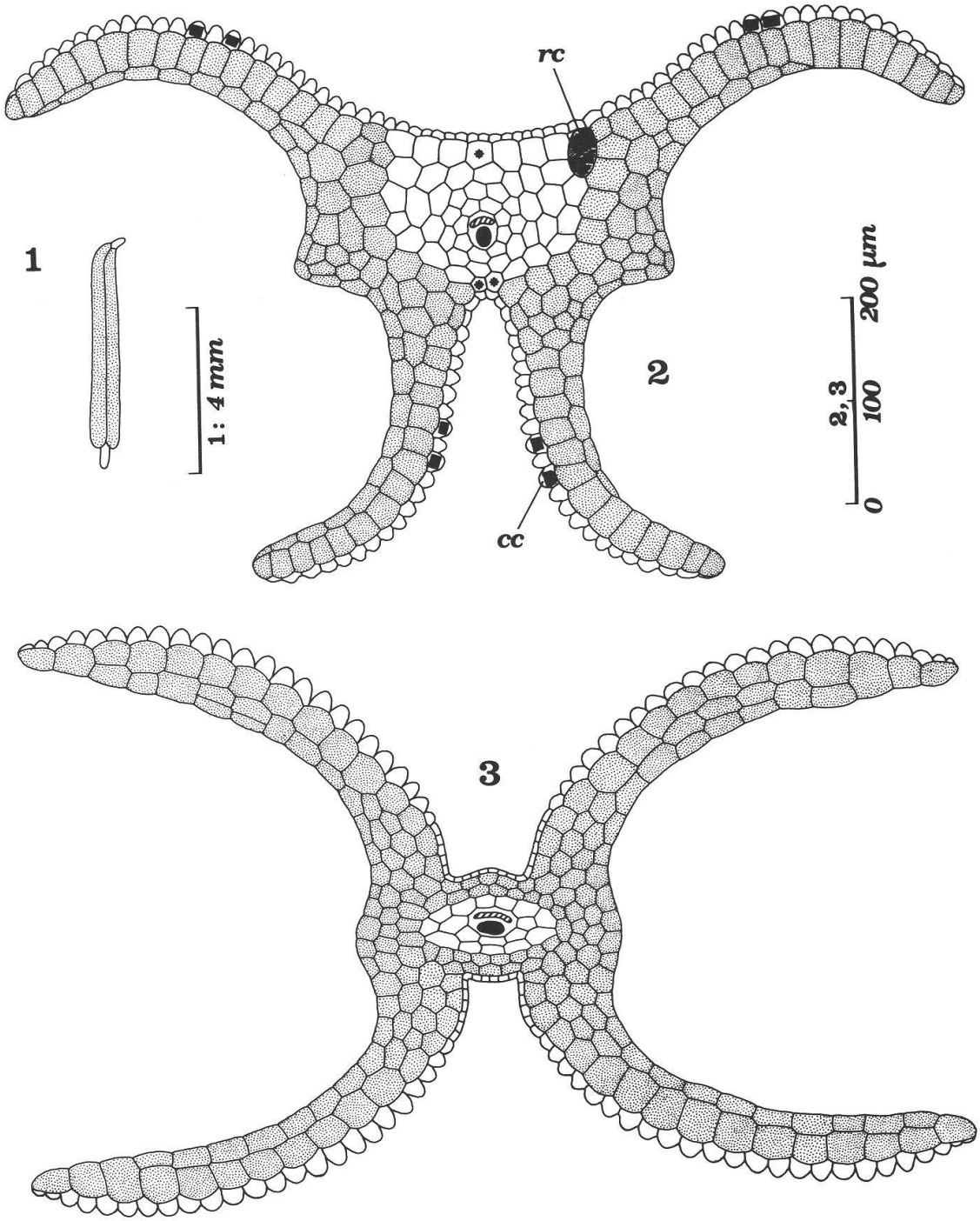

Fig. 1–3. *Pandanus eydouxia* (Fig. 1 and 2: *Lalouette MAU.12703*) and *P. utilis* (Fig. 3: *Michaux* s. n.). — Fig. 1: stamen. — Fig. 2: median transverse section of anther, showing abaxial epidermis above, cells with endothecial thickenings (dotted), phloem (hatched), xylem (black), crystal cell (*cc*) and raphide cell (*rc*) (asterisked: these three cells showed endothecial thickenings in some other transverse sections). — Fig. 3: median transverse section of anther, showing cells with endothecial thickenings (dotted), phloem (hatched) and xylem (black).

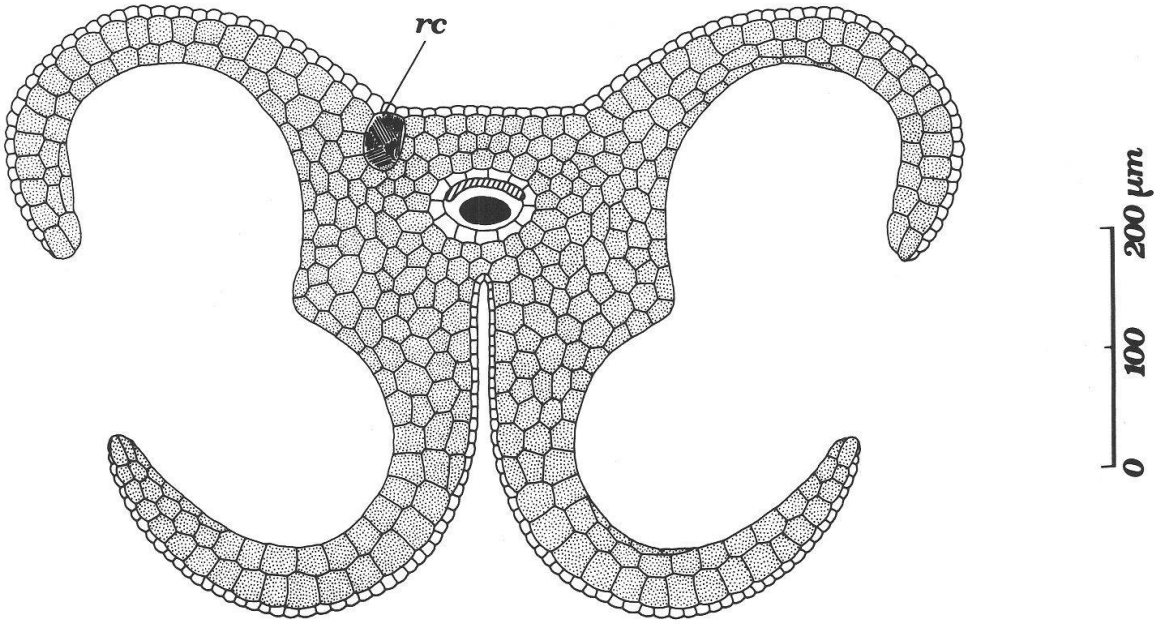

Fig. 4. *Pandanus spiralis:* median transverse section of anther, showing cells with endothecial thickenings (dotted), phloem (hatched), xylem (black) and raphide cell (*rc*).

by some other cells with endothecial thickenings, these cells being arranged in one layer and located just beneath the middle of this epidermis. But in no sections is the parenchyma completely separated from the abaxial epidermis by cells with endothecial thickenings. On the other hand – and this is for information, not to be taken into consideration in this comparison –, both anther loci are completely surrounded by layers of cells with endothecial thickenings, and the outer walls of the loci generally comprise one or two layers of such cells (Fig. 2).

In both *P. utilis* (Fig. 3) and *P. spiralis* (Fig. 4), on the contrary, the connective parenchyma around the vascular bundle is formed of 1 or 2 cell layers and completely separated from both epidermises by 2 or 3 layers of cells with endothecial thickenings. All the other species of subgenus *Vinsonia* that were studied showed the same anther structure as *P. utilis*. Likewise, all the other species of subgenus *Pandanus* that were studied (incl. *P. odoratissimus,* the type species of the subgenus) showed the same anther structure as *P. spiralis*. Thus, the anther structure of *P. eydouxia* indicates that this species does not fit any of these two subgenera. Furthermore, both anther loci in both *P. utilis* and *P. spiralis* are also completely surrounded by layers of cells with endothecial thickenings, but the outer walls of the loci generally comprise two or three layers of such cells (Fig. 3 and 4).

Finally, the anther acumen of *P. eydouxia* has cells with endothecial thickenings almost up to its apex. In other Mascarene species, such as *P. carmichaelii* Reg. Ed. Vaughan & Wiehe and *P. rigidifolius* Reg. Ed. Vaughan & Wiehe, only the lower half of the anther acumen has such cells. This feature seems to have no important taxonomic significance but may be used as a specific character.

2. Data from pollen morphology

The genus *Pandanus* generally has spinulose pollen (Erdtman 1952; Huynh 1980, 1982). In some groups, however, the pollen is smooth: this is the case in sections

Martellidendron (Huynh 1981), *Lophostigma* (Brongn.) Warb., *Barrotia* (Brongn.) Stone, *Maysops* St. John, *Karuka* Stone and *Asterostigma* Martelli (Huynh 1982), and in *P. pendulinus* Martelli which represents an unknown section (Stone & Huynh 1983). Furthermore, in *P.* sect. *Cauliflora* subsect. *Cauliflora* the pollen is slightly verrucate (Huynh & Stone 1981).

The pollen of *P. eydouxia* was studied with light microscopy by Erdtman (1952), but this method apparently did not facilitate the observation of the pollen sculpture. In fact, Erdtman (1952: 307) wondered if the pollen sexine of *P. eydouxia* was retipilate, i.e. "with a reticuloid pattern with pila instead of muri" (Erdtman 1952: 468). The scanning electron microscopy revealed that the pollen of this species was smooth and had muri, but the tectum did not extend to the lumina between these (Fig. 5, 6 and 9: for Fig. 9, note the left downwards-pointing arrow). In a certain percentage of grains, however, the pollen surface showed muri, bacula and processless nexine (Fig. 7 and 8). This partially defective formation of sexine remains to be explained but seems to be a feature of this species as such grains were observed in all the specimens studied and since these all bore fully mature stamens. In both subgenus *Vinsonia* and subgenus *Pandanus,* on the contrary, all of the species whose pollen morphology was studied with scanning electron microscopy and/or light microscopy by the present author (e.g. *P. utilis, P. pygmaeus* Thouars, *P. sambiranensis* Martelli, *P. borbonicus* Huynh, etc. for the former subgenus, and *P. odoratissimus, P. spiralis,* etc. for the latter) showed spinulose pollen with a perfect tectum (Fig. 11–13) (Huynh 1980: pl. I–III; Huynh 1983c: Fig. 31), except for *P. carmichaelii* (subgenus *Vinsonia*). The pollen of this Mauritian species, indeed, had "sexine consisting of ± piloid excrescences" (Erdtman 1952: 307), hence it is intectate, and this feature was confirmed with electron microscopy by the present author.

The pollen grain of *P. eydouxia,* as described above, is probably unique in the genus, considering the fact that the tectum is lacking on the lumina (Fig. 5, 6 and 9). These are, therefore, open lumina. In this respect, the pollen of this species only resembles, as far as known in the family Pandanaceae, the pollen of *Sararanga sinuosa* Hemsley, which shows "an outer layer comprising numerous roof openings, ..., with a complete absence of spines or distinct roof plates" in scanning electron microscopy (North & Willis 1971: 415; plate 1, E). Within *Pandanus,* in so far as known, it may only be compared to some degree with the pollen of *P.* subg. *Martellidendron* sect. *Martellidendron,* which has ± open lumina (Huynh 1981: Fig. 49–54). Despite the fact that *P. eydouxia* is clearly separated from the species of this Madagascan section by its drupe characters, staminate flower and anther structure, this similarity, although not close, between the pollen of the former species and that of the latter may indicate some relationship between them, especially as both have more or less the same geographic distribution. Furthermore, the unusual sculpture of the pollen grain of *P. eydouxia* (Fig. 5 and 6) may also explain why the aperture of this species was "often difficult to detect" (Erdtman 1952: 308) by light microscopy: this feature further emphasizes the isolation of *P. eydouxia* in the genus.

3. Data from fruit structure

A noticeable feature of the drupe of *P. eydouxia* consists in the fact that the basal part of the lower mesocarp apparently becomes hard and bony at maturity and in both structure and appearance is much like the endocarp, as was observed in *Bernardi 14869* (Fig. 10). As a result, the fibres in the basal part of the lower mesocarp are not free from one another – that is to say: they may not be separated without being broken or destroyed – as they usually are in the genus *Pandanus*. The fibres in the endocarp too are not free

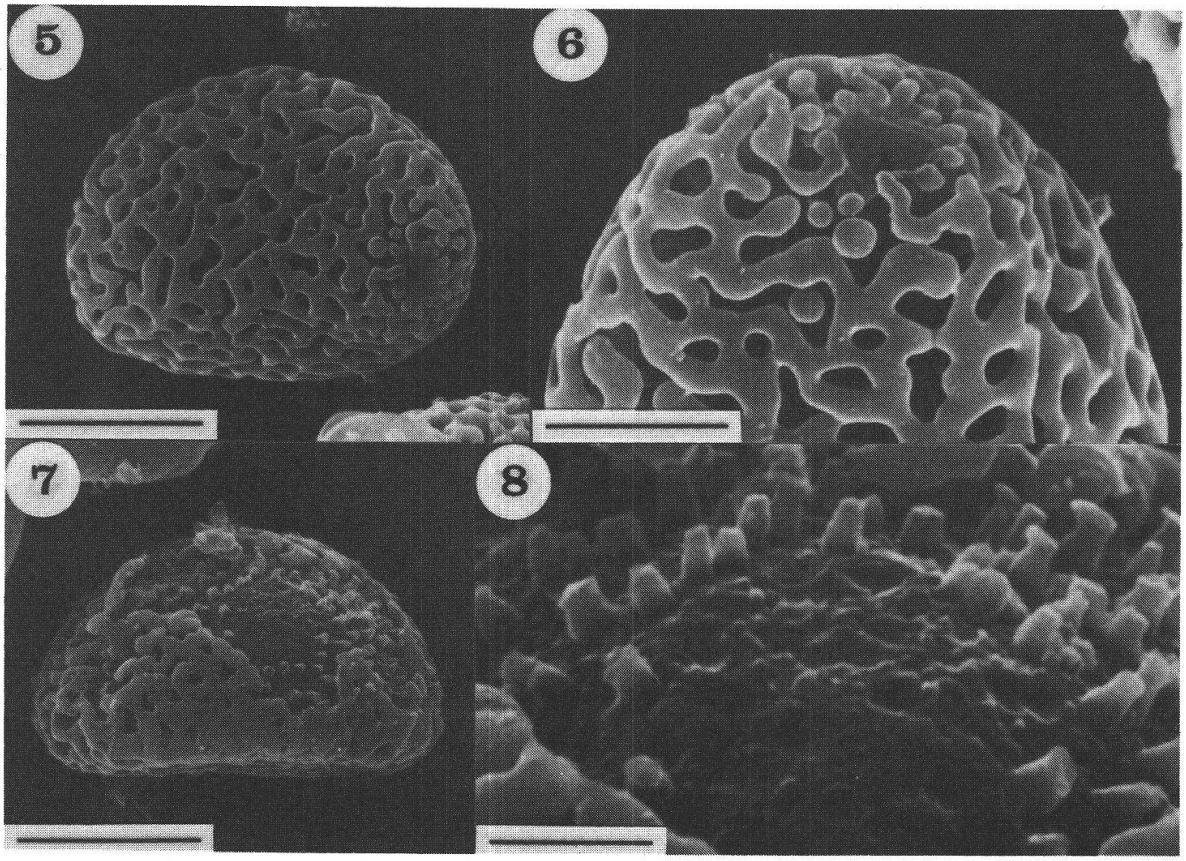

Fig. 5–8. *Pandanus eydouxia* (*Lalouette MAU.12703*) (SEM). — Fig. 5: pollen grain, showing aperture on right (scale bar = 10 μm). — Fig. 6: right part of pollen grain on Fig. 5, magnified, showing aperture above (scale bar = 5 μm). — Fig. 7: defective pollen grain (scale bar = 10 μm). — Fig. 8: right-central part of pollen grain on Fig. 7, magnified, showing bacula and processless nexine (scale bar = 2 μm).

because this is bony. On the contrary, the fibres in both the upper part of this mesocarp and the upper mesocarp are free, both of these being not bony. The only structural difference between the basal part of the lower mesocarp and the endocarp that could be observed is that the former is not as dark brown as the latter.

4. The taxonomic position of Pandanus eydouxia

As shown above, both the anther structure and the pollen morphology of *P. eydouxia* indicate that it does not belong in either subgenus *Pandanus* or subgenus *Vinsonia*. Neither can it find a suitable position in any other known subgenus, at least with the present state of knowledge. The isolated position of *P. eydouxia* is further shown by the fruit feature described above: the basal part of the lower mesocarp becomes bony at maturity. For these reasons, a new subgenus is erected for accommodating this species:

Pandanus subg. *Eydouxia* (Gaudich., pro gen.) (St. John, pro sect.) Huynh, stat. nov.
Basionym: *Eydouxia* Gaudichaud, Bot. Voy. Bonite: tab. 18. 1843; St. John, Pacific Sci. 16: 414. 1962.
Type: *Pandanus eydouxia* Balf. f.

It seems useful to indicate here the diagnostic characters of subgenus *Eydouxia* for further suitable identification and classification:

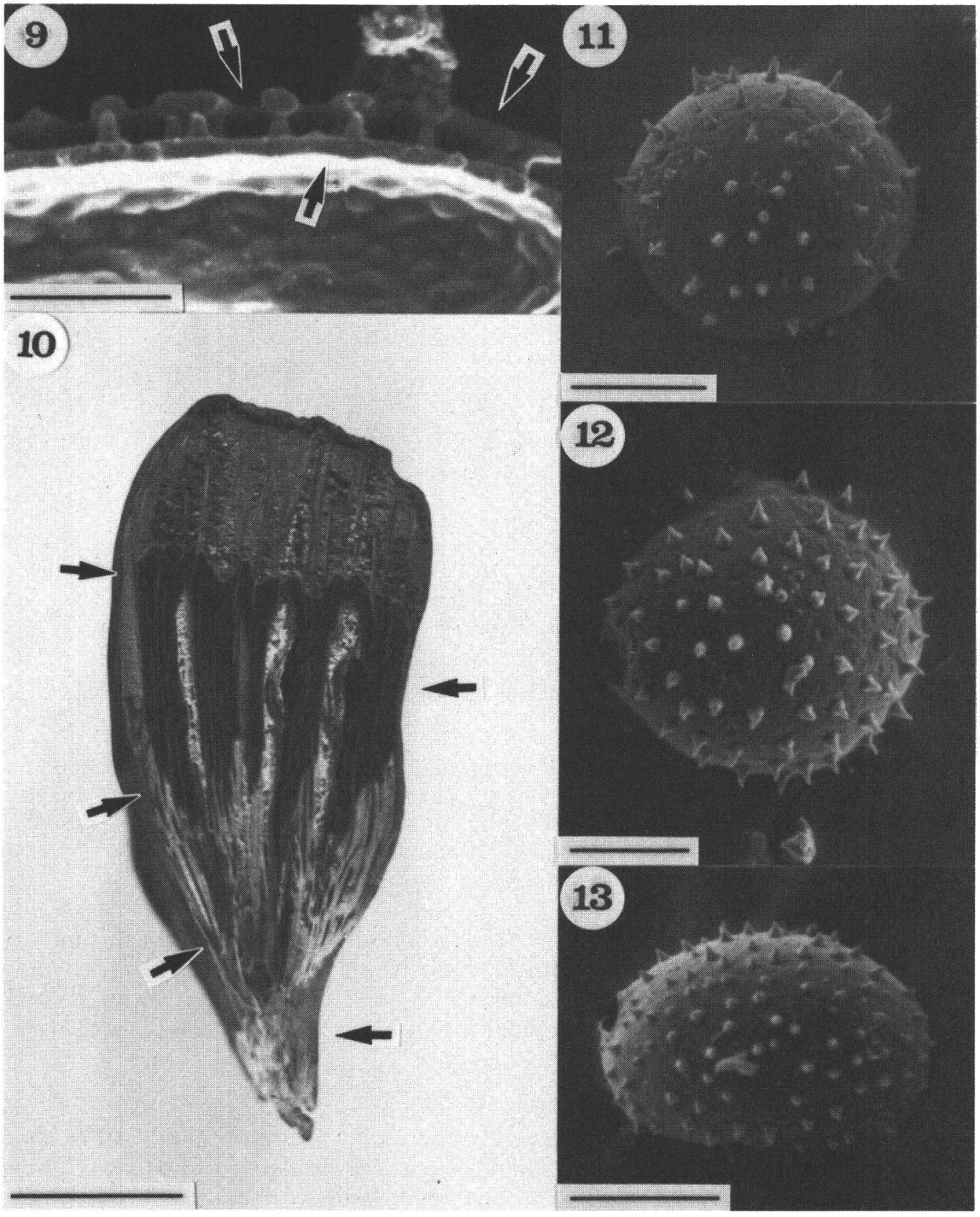

Fig. 9–13. *Pandanus eydouxia* (Fig. 9: *Lalouette MAU.12703;* Fig. 10: *Bernardi 14869*), *P. utilis* (Fig. 11: *Michaux* s. n.), *P. odoratissimus* (Fig. 12) and *P. spiralis* (Fig. 13). — Fig. 9: pollen-wall section, showing open lumen (left downwards-pointing arrow) (other open lumina also visible), murus (right downwards-pointing arrow) and nexine (upwards-pointing arrow) (scale bar = 5 µm) (SEM). — Fig. 10: median longitudinal section of drupe at shortest diameter (drupe about twice as wide as thick), showing left rim of section (rightwards-pointing arrows) and bony parts of drupe, these being endocarp (upper leftwards-pointing arrow) and basal part of lower mesocarp (lower leftwards-pointing arrow) (scale bar = 2 cm) (Photo). — Fig. 11: pollen grain (scale bar = 10 µm) (SEM). — Fig. 12 and 13: pollen grains, each showing aperture on left (scale bars = 10 µm) (SEM).

Trees; the syncarps solitary; the drupes large, unlobed, each formed of several flat-topped carpels; the basal part of the lower mesocarp bony, hard; the stamens of the staminate flower racemosely arranged along the upper part of the flower column; the connective parenchyma in the anther transverse sections never completely separated from the abaxial epidermis by cells with endothecial thickenings; the pollen smooth, with open lumina.

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