

Sze Peng CHU* & Benjamin C. STONE*: **Morphological studies in Pandanaceae V.**

A further survey of foliar anatomy
in the genus *Pandanus*** (1)

S. P. チュー*・B. C. ストーン*: タコノキ科の形態学的研究 V.

タコノキ属の葉の解剖学的研究 (1)

Previous work and methods of study in correlating micromorphological and gross-morphological characters with a view to improving natural classification in *Pandanus* is thoroughly discussed in Kam (1969, 1971) and Kam & Stone (1970).

The present study extends these methods to twenty-three further species of *Pandanus*, which are listed, together with voucher data, in Table 1. Of these living material was used for *P. crinifolius*, revived herbarium materials for the remainder. Standardized segments from adult leaves of adult plants were used. Peels, for epidermal study, and longitudinal and transverse sections, were the main sources of information.

The general morphology and relevant aspects of developmental morphology are discussed sufficiently by Kam (1971).

Results

Stomatal structure

Class 1: Unspecialized stomata. For definition, see Kam (1971) and Tomlinson (1965). Generic section of species noted parenthetically.

P. crinifolius (Rykia)

P. fragrans (Pandanus)

P. spinistigmaticus (Rykia)

P. cominsii (Microstigma)

Class 2: Stomata with papillose lateral subsidiary cells.

P. kaida (Pandanus)

P. simplex (sect. incert.)

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** Based on a University of Malaya Honours Botany Project 1970/71, by the first author. See Part III, by Y. K. Kam, in Bot. J. Linn. Soc. 64(4): 315-351, 1971; and Part IV, by Kam & Stone, in *Adansonia* ser. 2, 10(2): 219-246, 1970.

It should be noted here that in *P. simplex* the terminal subsidiary cells are just showing papillae; the guard cells and lateral subsidiary cells are not sunken. Papillae are developed however on the neighboring epidermal cells. These are arranged in irregular rings of various sizes, enclosing one to many stomata. Still other stomata are not so enclosed. The result is a very characteristic appearance (cf. Fig. 21).

Class 3: Papillose terminal and lateral subsidiary cells.

P. vinaceus (Asterostigma) *P. myriocarpus* (Heterostigma)

Table 1. Species studied, source of materials, voucher specimens.
(Herbarium abbreviations follow Index Herbariorum).

Species of <i>Pandanus</i>	Source area	Voucher specimen
<i>ambongensis</i> Martelli	Madagascar	Guillaumet 2235 (KLU)
<i>bowersae</i> St. John	New Guinea	Bowers 766 (KLU)
<i>clarkei</i> B. C. Stone	New Guinea	Clarke 108 (KLU)
<i>clementis</i> Merrill	Philippines	Hernaiz 4010 (CAHP)
<i>cominsii</i> Hemsl. var. <i>micronesicus</i> Stone	Truk, Micronesia	Stone 5340 (KLU)
<i>crinifolius</i> Martelli	Malaya	Stone 6258 (KLU)
<i>danchelmannianus</i> K. Schum.	New Guinea	Clarke 126 (KLU)
<i>eydouxia</i> Balf. f.	Mauritius	Stone 7705 (KLU)
<i>fragrans</i> Gaudich.	Guam	Stone 4248 (GUAM)
<i>gibbsianus</i> Martelli	Sarawak	Stone 6763 (KLU)
<i>kaida</i> Kurz	Cambodia	Stone 9318 (KLU)
<i>kirkii</i> Rendle	Tanzania	Stone 7734 (KLU)
<i>longipedunculatus</i> Fagerl.	Celebes	Kjellberg 2292 (S)
<i>magnificus</i> Martelli	New Guinea	Clarke 34 (KLU)
<i>multifurcatus</i> Fagerl.	Java	Stone 8445 (KLU)
<i>matthewsii</i> Merrill	Sabah	Stone 6690 (KLU)
<i>myriocarpus</i> Baker	Madagascar	Guillaumet 2275 (KLU)
<i>pectinatus</i> Martelli	Sarawak	Anderson (SAR)
<i>platystigma</i> Martelli	Sarawak	Stone 6780 (KLU)
<i>simplex</i> Merrill	Philippines	Pancho 5590 (KLU)
<i>spinistigmaticus</i> Fagerl.	Java	Stone 8448 (KLU)
<i>vinaceus</i> B. C. Stone	Sarawak	Stone 6774 (KLU)
sp. (Maysops)	New Guinea	Clarke 121 (KLU)

In both these species a few papillose neighboring epidermal cells may be seen, showing an approach to the Class 4 type.

Class 4: Papillose neighboring and subsidiary cells.

- P. multifurcatus* (Rykia) *P. pectinatus* (Acrostigma)
P. clarkei (Paralophostigma) *P. clementis* (Jeanneretia)
P. bowersae (Excavata) *P. longipedunculatus* (Rykiopsis)
P. kirkii (Pandanus) *P. ambongensis* (Heterostigma)
P. magnificus (Microstigma) *P. sp.* (Maysops)

Table 2. Stomatal size and density in 23 species of *Pandanus*.

Species of <i>Pandanus</i>	Stomatal size (μ^2)	Stomatal Density per mm^2		Stomatal Class (Abaxial)	Section
		Abaxial/ Adaxial			
<i>simplex</i>	294.9	4.6	0.4	2	Utilissima
<i>clarkei</i>	255.2	8.8	0.3	4	Paralophostigma
<i>pectinatus</i>	236.1	16.9	0.0	4	Acrostigma
<i>myriocarpus</i>	223.3	13.6	6.8	3	Heterostigma
<i>fragrans</i>	201.0	24.4	0.9	1	Pandanus
<i>spinistigmaticus</i>	191.4	21.4	0.4	1	Rykia
<i>crinifolius</i>	184.6	6.5	0.0	1	"
<i>bowersae</i>	180.9	28.0	3.9	4	Pandanus
<i>kirkii</i>	155.2	22.0	0.2	4	"
<i>platystigma</i>	148.8	15.3	0.0	5	Pseudacrostigma
<i>ambongensis</i>	148.8	17.4	0.2	4	Heterostigma
<i>cominsii</i>	138.3	16.7	0.5	1	Microstigma
<i>magnificus</i>	130.2	21.2	0.5	4	Microstigma
<i>kaida</i>	127.3	25.9	1.7	2	Pandanus
<i>longipedunculatus</i>	119.7	17.2	0.5	4	Rykiopsis
<i>multifurcatus</i>	106.4	25.9	1.7	4	Rykia
<i>gibbsianus</i>	106.4	5.1	0.8	5	Acrostigma
<i>eydouxia</i>	106.4	14.6	0.6	5	Eydouxia
sp. (Maysops)	90.0	19.0	0.9	4	Maysops
<i>danckelmannianus</i>	95.7	27.6	1.4	5	Acrostigma
<i>vinaceus</i>	85.1	17.3	0.7	3	Asterostigma
<i>matthewsii</i>	73.2	12.1	1.8	5	"
<i>clementis</i>	63.8	29.8	0.5	4	Jeanneretia

In *P. clementis*, *P. longipedunculatus*, *P. sp.*, and *P. ambongensis*, the papillae are slightly lobed, indicating a slight transitional state to Class 5.

Class 5: Overarching papillae lobed or dendritic.

P. matthewsii (Asterostigma) *P. eydouxia* (Eydouxia)

P. danckelmannianus (Acrostigma)

P. gibbsianus (Acrostigma) *P. platystigma* (Pseudacrostigma)

Stomatal size and frequency

Stomatal size in the species studied ranges from about 64μ (*P. clementis*) to 295μ (*P. simplex*). Density varies from 4.6 to 29.8 stomata per mm^2 (abaxial epidermis). In general, leaves with smaller stomata have greater stomatal density. Specialized stomata (Classes 3-5) tend to be smaller than unspecialized ones. In *P. eydouxia*, with Class 5 stomata, the stomate size is about 106μ ; in *P. simplex*, with Class 2 stomata, the stomate size is about 295μ . In Sect. Pandanus and Sect. Asterostigma, the species studied have about equal stomatal density and stomatal size. In Sect. Rykia, *P. crinifolius* and *P. spinistigmaticus* have about the same stomate size but very different density values. This is also true in Sect. Acrostigma of *P. danckelmannianus* and *P. gibbsianus*.

Stomatal class is not completely constant within sections. However, in some sections, there is rather little variation, e. g. in Sect. Acrostigma, the species studied up till now are almost all of Class 4 or Class 5.

Anatomical notes on the species

(1) Costal vs. intercostal differentiation (zones) on abaxial epidermis. About half the species studied showed this zonal differentiation. In *P. matthewsii* (Asterostigma) it is very distinct, while in *P. fragrans* (Pandanus) it is slight. In *P. spinistigmaticus* (Rykia) it is absent. *P. eydouxia* and *P. platystigma* have, in costal regions, epidermal cells with wavy (sinuous) anticlinal walls while cells of the intercostal regions have straight walls.

(2) Hypodermis. In *P. clarkei* and *P. gibbsianus* both the abaxial and adaxial hypodermal cells are pitted (Figs. 9, 41). Crystals are present.

(3) Fibres. In *P. clarkei* unligified fibres are concentrated just below the hypodermis. In *P. matthewsii* where this is also the case, the fibres are few, but in *P. platystigma* there are numerous such fibres in groups (of up to 16).

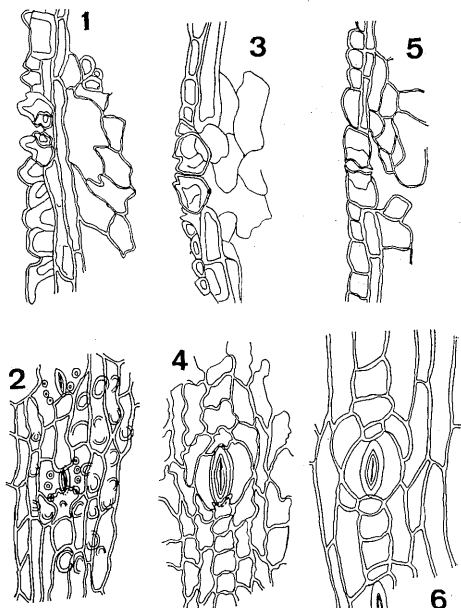
In *P. pectinatus* the fibres occur as compact groups of 16-50, in strands

abundant in the spaces between the vascular bundles (Fig. 45).

(4) Vascular bundles. In all the species the vascular bundle structure is fairly similar. Usually 1 or 2 large metaxylem vessels are separated from the protoxylem by xylem parenchyma cells and phloem of sieve tubes and companion cells. Bundle sheaths may be present, which may form vertical extensions to the hypodermis.

(5) Crystals. Raphidophorous cells are often found in the edges of the palisade layers. Rhomboidal crystals appear to occur in one of 2 forms: one form has striations across the face, as noted in *P.*

sp. (Maysops), while the other form has a plain surface, as in *P. kaida*. Where the epidermis is zoned, the crystals are mainly found within the costal zone. In *P. clementis* (Jeanneretia) there is a quite remarkable abundance of crystals, found as transverse rows of 2-17 in the hypodermal layers, round the vascular bundles and associated with fibrous strands in mesophyll. In *P. eydouxia* they occur singly in outer hypodermis. In *P. myriocarpus* they are lacking in hypodermis but occur around VB's and in the mesophyll. In *P. ambongensis* they are absent from upper hypodermal layer but a few occur in the lower hypodermal layer.



Figs. 1-6. 1-2: *Pandanus multifurcatus* (1: T.S. of stomate; 2: epidermal surface showing stomatal complex). 3-4: *P. spinistigmaticus* (3: T.S. of stomate; 4: epidermal surface and stomate). 5-6: *P. crinifolius* (5: T.S. of stomate; 6: epidermal surface with stomate).

Systematic treatment

Genus *Pandanus*

Sect. *Rykia* (DeVr.) Kz.

P. multifurcatus Fagerlind. (Figs. 1-2)

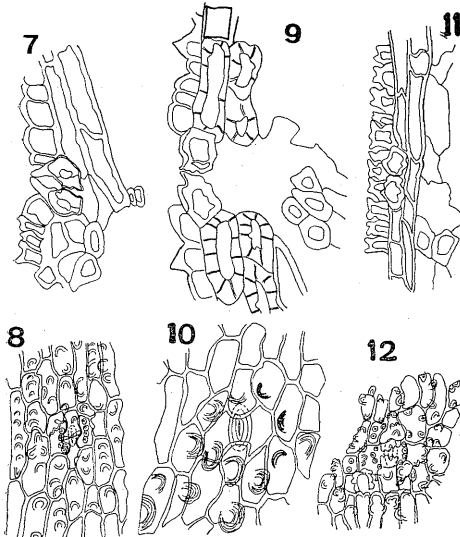
Costal-intercostal differentiation vague. Epidermal cells rectangular in surface view, some papillose; papillae simple, 1-3 per cell. Stomata: Class 4, not sunken. Hypodermis: 2-layered both ad- and abaxially. Rhomboidal crystals in rows of 1-3 in costal, abaxial hypodermis, in and round VB's and in spongy mesophyll. Mesophyll palisade with isolated strands of fibres of 2-3 each. Raphides in both palisade layers.

P. spinistigmaticus Fagerlind. (Figs. 3-4)

Costal-intercostal differentiation none. Epidermal cells rectangular in surface view, with sinuous anticlinal and end walls, not papillose. Stomata: Class 1. Hypodermis: 2-layered ad- and abaxially. Rhomboidal crystals few in hypodermis and mesophyll. Palisade with isolated fibrous strands. Raphides none.

P. crinifolius Martelli. (Figs. 5-6)

Costal-intercostal differentiation absent. Epidermal cells rectangular in surface view, nonpapillose. Stomata: Class 1. Hypodermis: 2-layered ad- and abaxially. Rhomboidal crystals in adaxial hypodermis, in transverse rows of 2-4 (common) or 5 (rare), also randomly in mesophyll. Palisade with fibres in upper palisade layers. Raphides none.



Figs. 7-12. 7-8: *Pandanus longipedunculatus* (7: T. S. of stomate; 8: epidermal surface with stomate and papillae). 9-10: *P. clarkei* (9: T. S. of stomate; 10: surface of epidermis with stomate and papillae). 11-12: *Pandanus* sp. (Sect. Maysops). (11: T. S. of stomate and papillae; 12: epidermal surface with stomate and papillae).

Comments: It is noteworthy that *P. multifurcatus* stands a little apart because of its wavy cell walls, zoned epidermis, rather elaborate stomata, and crystal arrangement. This reinforces the inclusion of this species in a distinct taxon, originally Sect. *Multipinna* Fagerlind, now

treated as Sect. *Rykia* subsect. *Multispina* (Fagerl.) Stone.

Sect. *Rykiopsis* B. C. Stone

P. longipedunculatus Fagerlind. (Figs. 7-8)

Abaxial epidermis zoned. Epidermal cells papillose but only in intercostal regions. Papillae slightly lobed, 2-8 per cell. Stomata: Class 4, transitional to Class 5. Hypodermis: 2-layered abaxially, 3-layered adaxially. Rhomboidal crystals very few, in hypodermal layers and around VB's. Mesophyll palisade with few fibrous strands.

Comments: The anatomical features of this species somewhat resemble those of *P. yvanii*, *P. helicopus*, and *P. militaris* as described by Kam (1969, 1971). The habitat is similar in all cases. Sect. *Rykiopsis* is closely related to Sect. *Solmsia*.

Sect. *Paralophostigma* B. C. Stone

P. clarkei B. C. Stone. (Figs. 9-10)

Costal-intercostal differentiation none. Epidermal cells rectangular in surface view, papillose. Stomata: Class 4, not sunken. Hypodermis: 2-layered ab- and adaxially, cells long, narrow, thick-walled, pitted. Rhomboidal crystals in outer hypodermal layers in transverse rows of 1-6 (abaxially) or 1-3 (adaxially), also present around VB's and in mesophyll. Mesophyll non-palisade, isolated bundles of fibres immediately below hypodermal layers. Raphides present.

Sect. *Maysops* St. John

Pandanus sp. (Clarke 121). (Figs. 11-12)

Epidermis not zoned. Epidermal cells papillose, papillae dendritic, 1 per cell. Stomata: Modified Class 4; occurring in interlocking 'chains'. Hypodermis: 3-layered on both surfaces. Rhomboidal crystals single or in rows of 1-3 in outer hypodermal layers and around and in VB's and mesophyll. Mesophyll palisade with fibres and raphides.

Comments: The peculiar distribution of the stomata in interlocking 'chains', and the abundance of rhomboidal crystals are noticeable in this species. The crystals seen have a striated surface not noticed in other species so far.

Sect. *Asterostigma* Martelli

P. matthewsii Martelli. (Figs. 13-14)

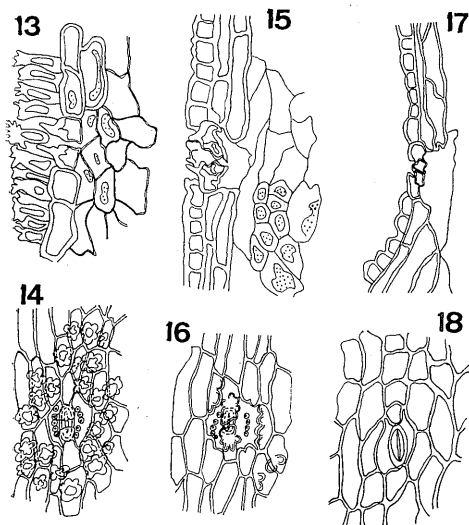
Costal-intercostal differentiation very distinct. Epidermal cells papillose only in intercostal region, papillae dendritic, 1-2 per cell, overarching stomata. Stomata: Class 5, restricted to intercostal zone. Hypodermis: 2-layered adaxially, absent abaxially, cells do not have spindle shape (but are short, broad). Rhomboidal crystals very few in hypodermis palisade, and around VB's. Mesophyll palisade with few fibres occurring singly. Raphides absent.

P. vinaceus B. C. Stone. (Figs. 15-16)

Costal-intercostal differentiation absent. Only a few neighboring epidermal cells papillose, papillae simple. Stomata: Class 3, but a few developing to Class 4. Hypodermis: 2-layered adaxially and 3-layered abaxially. Rhomboidal crystals few in hypodermal layers, palisade layers,

and around VB's. Mesophyll palisade with abundant groups of fibres of 2-10 each. Raphides absent.

Comments: Kam (1969, 1971) reports that in *P. pentodon*, a member of Sect. *Asterostigma*, the epidermis is vaguely zoned, the epidermal cells are all papillose, and the rhomboidal crystals are abundant. It is noticeable that the two species described above differ in these respects. They conform however in having elaborate stomata (Class 5) and short, broad, hypodermal cells. *P. vinaceus* is the most distinct species in the section; this distinc-



Figs. 13-18. 13-14: *Pandanus matthewsii* (13: T.S. of stomate; 14: epidermal surface with papillae). 15-16: *P. vinaceus* (15: T.S. of stomate; 16: epidermal surface with stomate). 17-18: *P. cominsii* var. *micronesicus* (17: T.S. of stomate; 18: epidermal surface with stomate).

tiveness appears also in regard to leaf anatomy.

Sect. *Microstigma* Kurz.

P. cominsii Hemsl. var. *micronesicus* B. C. Stone. (Figs. 17-18)

Epidermis not zoned. Epidermal cells non-papillose. Stomata: Class 1. Hypodermis: 2-layered both ad- and abaxially. Rhomboidal crystals quite abundant in outer hypodermal layers and mesophyll. Palisade with fibrous strands. Abaxial hypodermis and palisade layers interrupted by substomatal chambers. Raphides in adaxial palisade.

Comment: This species has a very uniform epidermis, greatly contrasting with that of *P. simplex*, which had been placed in the same section.

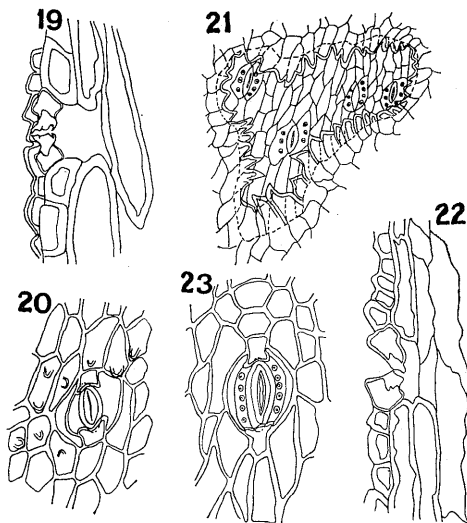
P. magnificus Martelli. (Figs. 19-20)

Epidermis not zoned. Some epidermal cells papillose, with simple papillae, one per cell. Stomata: Class 4. Hypodermis: 3-layered abaxially, 5-layered adaxially. Rhomboidal crystals quite abundant in transverse rows of 1-5 or more in outer hypodermal layers, also around VB's and in mesophyll. Mesophyll thinly palisade layered in lamina, not in midrib region, with very few small fibrous bundles. Raphides present.

Sect. *Utilissima* B. C. Stone

P. simplex Merrill (= *P. utilissimus* Elmer). (Figs. 21-23)

Costal-intercostal differentiation absent. Epidermal cells rectangular in surface view, papillae developed in epidermal neighboring cells in such a way as to form ir-



Figs. 19-23. 19-20: *Pandanus magnificus* (19: T.S. of stoma; 20: epidermal surface with stoma). 21-23: *P. simplex* (21: stomatal group within "stockade" of papillae; 22: T.S. of stoma; 23: epidermal surface with stoma).

regular "stockades" enclosing up to 20 stomata (Fig. 21). Stomata not enclosed by such "stockades" are either Class 1 or transitional to Class 2, with papillae developed on only one lateral subsidiary cell. Enclosed stomata are all of Class 2. A few Class 1 stomata have one of the lateral subsidiary cells divided into two. Hypodermis: 4-5-layered both ad- and abaxially, with outer layer consisting of shorter cells. Rhomboidal crystals quite abundant in outer hypodermal layers, around VB's and in mesophyll. No palisade. Mesophyll with fibrous strands among chlorenchymatous cells. Raphides present.

Comment: See remarks on *P. cominsii*.

(To be continued)

□Reprint, microfiche and new supplement of Saccardo's *Sylloge Fungorum*

(1882-1972) サッカルドのシローゲ・フンゴールム覆刻版, マイクロフイッシュおよび補遺新刊. Johnson Reprint Corporation, 111 Fifth Avenue, New York, N. Y. 10003. 日本代理店: John Weatherhill, Inc. 東京, 港区, 六本木 7 丁目 6-13.

数年前に P. A. Saccardo の 25 巻 (28 冊) の覆刻版が出た当時は私共菌学徒は驚喜したことがある。僅々 1,130\$ の廉価であり, 安自動車一台にも足りぬ金額のため, 個人でも入手可能となった訳である。これで真菌類のうち 78,361 種のラテン記載が手元で見られるようになったのである。しかし今回これのマイクロフイッシュが只の 180\$ で購入出来る由であるから, 我々庶民学徒には重なる吉報である。単にそればかりではない。従来の 25 巻に加えて第 26 巻 (補遺) が只今出たという報告に接した。これは 1931 年以降はじめて出た補遺であり, 1950 年頃までに発表された約 5,000 種のラテン記載其他が採録されており, S 氏の養子 A. Trotter のノートから整理し, その子息の菌学者 G. B. Trotter 氏の前文もあるという。これに蛇足を加えることをおゆるし願いたい。昭和 16 年に満州に転任することになり, 私にとって一番必要な書物はこのシローゲであると思い, 当時東大にあった約 20 巻までの複写を思い立って, 植物教室の松尾写真師にこれを依頼した。約半年後に 8 巻まで完成したが, 遂に退職金も底をつき未完に終わった。そのため新京から汽車で一時間ほどの 公主嶺の農事試験所にこれを探べに出張すること屢々であった。今から 8 年ほど前に残りの分も覆写出来て四半世紀振りて手元で利用出来るようになった。往時を回想すると, 現在は何とめぐまれた時代かなと感慨深いものがある。因みに第 26 巻は 85\$ の由。 (小林義雄)