

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

A further survey of foliar anatomy
in the genus *Pandanus* (2)**

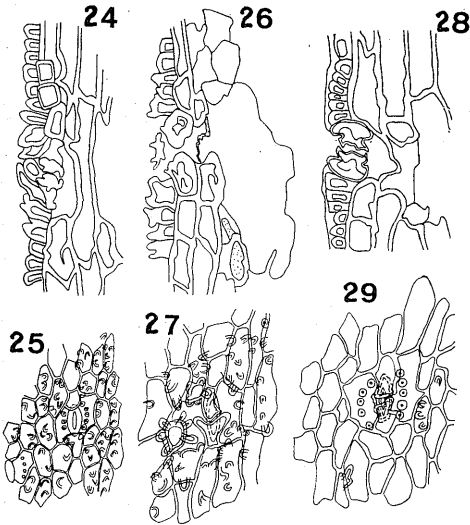
S. P. チュー*・B. C. ストーン*: タコノキ科の形態学的研究 V.
タコノキ属の葉の解剖学的研究 (2)**

Sect. *Jeanneretia* (Gaud.) B. C. Stone

P. clementis Merrill. (Figs. 24-25)

Costal-intercostal differentiation distinct. Epidermal cells papillose only in intercostal regions, with 1-3 papillae per cell, the papillae slightly lobed. Stomata: Class 4, but somewhat transitional to Class 5. Hypodermis: 3-layered on both surfaces. Rhomboidal crystals very abundant, in rows of 2-17 in outer hypodermal layers, also around VB's, in mesophyll, and associated with fibrous strands in mesophyll. No palisade. Raphides present.

Comments: Kam (1969, 1971) described leaf anatomy of *P. polycephalus* Lam., the type species of this section. *P. clementis* corresponds in most respects. Both species have the zoned abaxial epidermis,



Figs. 24-29. 24-25: *Pandanus clementis* (24: T. S. of stomate; 25: epidermal surface with stomate and papillae). 26-27: *P. ambongensis* (26: T. S. of stomate and papillae; 27: epidermal surface with stomate and papillae). 28-29: *P. myriocarpus* (28: T. S. of stomate; 29: epidermal surface with stomate).

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** Continued from J. J. B. 48: 55-64, 1973.

papilosity in some epidermal cells, and elaborate stomata confined to intercostal regions. Both species also show the striking abundance of rhomboidal crystals. This is a strong confirmation of consectional affinity.

Sect. *Heterostigma* (Gaud.) B. C. Stone

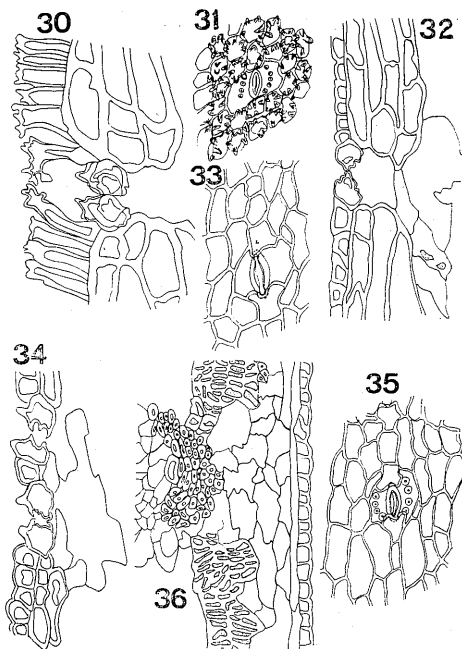
P. ambongensis Martelli. (Figs. 26-27)

Costal-intercostal differentiation present. Epidermal cells, papillose, slightly lobed. Papillae 1-5 per cell. Stomata: Class 4, or transitional to Class 5. Hypodermis: 3-layered abaxially, 2-layered adaxially. Rhomboidal crystals few, in lower hypodermal layers, around and in VB's, and a few associated with fibrous strands. Mesophyll thinly palisade with fibres. Mesophyll cells with wavy walls.

P. myriocarpus Baker.
(Figs. 28-29)

Costal-intercostal differentiation present. Epidermal cells mostly non-papillose but one or two in proximity of stomata with papillae. Stomata: Class 3, transitional to Class 4. Hypodermis: 3-layered abaxially, 4-layered adaxially. Rhomboidal crystals absent in hypodermis, a few present around VB's, numerous in mesophyll, some associated with fibrous strands. Mesophyll non-palisade, fibres in groups of 2-6. Mesophyll cells with wavy walls. Raphides none.

Comments: These two species are very similar. The elaborate stomata, mesophyll



Figs. 30-36. 30-31: *Pandanus eydouxia* (30: T. S. of stomate and dendritic papillae; 31: epidermal surface). 32-33: *P. fragrans* (32: T. S. of stomate; 33: epidermal surface and stomate). 34-36: *P. kaida* (34: T. S. of stomate; 35: epidermal surface with stomate; 36: partial T. S. of leaf adaxial epidermis and associated tissues).

cells with wavy walls, and distinct epidermal zonation, are good identifying features.

Sect. *Eydouxia* St. John

P. eydouxia Balf. f. in Baker. (Figs. 30-31)

Costal-intercostal differentiation distinct. Costal epidermal cells with wavy anticlinal walls and non-papillose. Intercostal epidermal cells papillose and with straight walls. Papillae dendritic, overarching stomata. Stomata: Class 5. Hypodermis 4-layered ab- and 6-layered adaxially. Rhomboidal crystals few, singly occurring in hypodermal layers, around and in VB's and in mesophyll. Palisade with fibres. Raphides none.

Comments: This species, the sole representative of its section, seems to be related to Sect. *Pandanus*. In anatomical characters there are re-

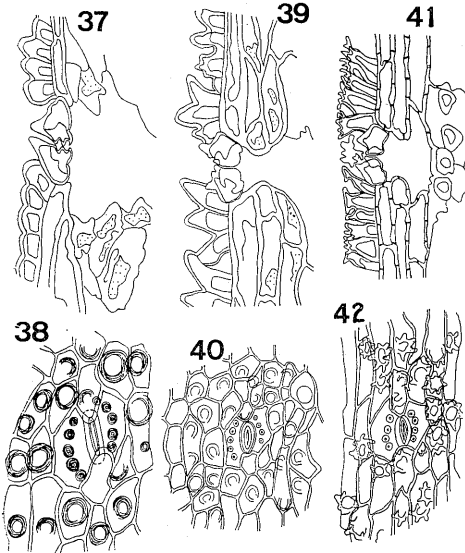
semblances to *P. kirkii*. However, the characteristic sinuous anticlinal walls in *P. eydouxia*, the elaborate stomata, and the multiseriate hypodermis confirm its considerable distinctness.

Sect. *Pandanus* s. s.

P. fragrans Gaudich.

(Figs. 32-33)

Costal-intercostal differentiation vague. Epidermal cells non-papillose. Stomata: Class 1. Hypodermis: 3-layered ab- and adaxially, interrupted by substomatal chambers. Rhomboidal crystals very few, occurring singly or in pairs in abaxial outer hypodermal layer, absent in adaxial hypodermis, also



Figs. 37-42. 37-38: *Pandanus kirkii* (37: T.S. of stomate; 38: epidermal surface with stomate, showing papillae). 39-40: *P. bowersae* (39: T.S. of stomate; 40: epidermal surface with stomate and papillae). 41-42: *P. gibbsianus* (41: T.S. of stomate, not long dendritic papillae; 42: epidermal surface with stomate and papillae).

present all around edge of VB's and in VB's, and in mesophyll but not in palisade layers. Mesophyll with distinct palisade layers, with fibrous strands ad- and abaxially. Raphides present.

P. kaida Kurz. (Figs. 34-35)

Costal-intercostal differentiation indistinct. Epidermal cells non-papillose. Stomata: Class 2. Hypodermis: 2-layered ab- and adaxially, interrupted by substomatal chambers. Rhomboidal crystals very few in abaxial outer hypodermal layer, around and in VB's and in palisade layers. Mesophyll with palisade, with fibrous strands in both ab- and adaxial layers. Raphides in mesophyll and palisade.

P. kirkii Rendle. (Figs. 37-38)

Costal-intercostal differentiation present. Epidermal cells papillose in intercostal zone only, papillae simple. Stomata: Class 4. Hypodermis: 2-layered abaxially and 3-layered adaxially. Rhomboidal crystals very few, occurring singly and in pairs in abaxial outer hypodermal layer, absent in adaxial hypodermis, a few around VB's, some associated with fibrous strands in mesophyll. Palisade layers distinct, fibres in groups of 1-8. Raphides present.

Comments: *P. kaida*, once associated with Sect. Hombronia, appears to pertain to Sect. Pandanus. It resembles *P. fragrans* in having unspecialized stomata, non-papillose epidermal cells, and absence of rhomboidal crystals. *P. kirkii* is somewhat set apart by its elaborate stomata and clear zonal differentiation.

Sect. Excavata B. C. Stone

P. bowersae St. John. (Figs. 39-40)

Epidermis not zoned. Epidermal cells all papillose, papillae simple and spiniform, 1-2 per cell. Stomata: Class 4. Hypodermis: 3-layered abaxially, 4-layered adaxially. Hypodermal cell about 2-6 times longer than epidermal cell. Rhomboidal crystals in transverse rows of 1-3 in outer hypodermal layers in VB's, palisade, and mesophyll. Fibres in groups of 2-3 or singly, in both palisade layers. Raphides abundant in mesophyll and at edge of both palisade layers.

Sect. *Acrostigma* Kurz

P. gibbsianus Martelli. (Figs. 41-42)

Costal-intercostal differentiation absent. Epidermis of long and short cells (surface view), the shorter cells papillose, the longer cells not so. Short papillose cells in 'chains' forming network around stomata. Papillae dendritic, 1-2 per cell, overarching stomata. Stomata: Class 5. Hypodermis 4-layered ad- and abaxially, walls pitted. Rhomboidal crystals few in outer hypodermal layers, abundant round edges of mesophyll and also in VB's. Mesophyll non-palisade; with conspicuous strands of fibres just below hypodermal layers, strands of 2-16 fibres, or more. Adaxial mesophyll cells with wavy anticlinal walls; abaxial cells lobed. Raphides few, in adaxial mesophyll.

P. pectinatus Martelli.

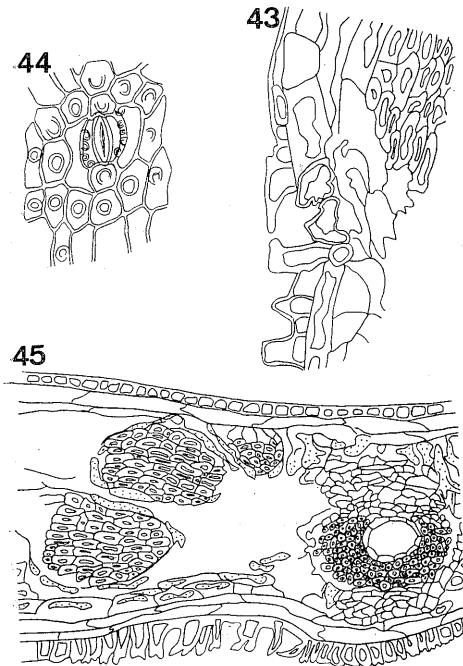
(Figs. 43-45)

Costal-intercostal differentiation distinct. Epidermal cells papillose in intercostal regions, papillae simple, 1 per cell. Stomata: Class 4. Hypodermis: 2-layered on both surfaces. Rhomboidal crystals few, in outer hypodermis layers, around VB's and near fibrous strands. Mesophyll non-palisade. Between VB's and in chlorenchyma occur distinct subcylindric strands of 16-50 fibres.

P. danckelmannianus K.

Schumann. (Figs. 46-47)

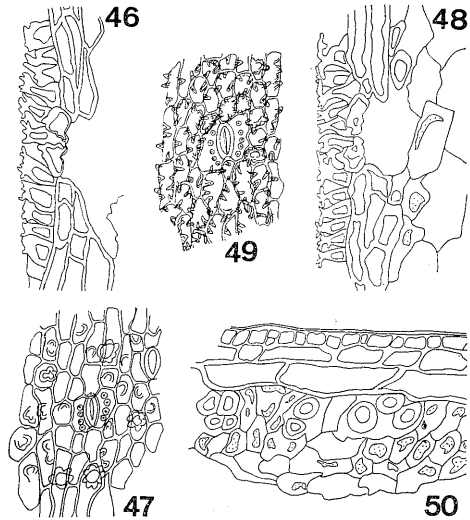
Epidermis not zoned. Some epidermal cells papillose with 1-2 papillae per cell, papillae dendritic, forming



Figs. 43-45. *Pandanus pectinatus* (43: T.S. of stomate; 44: epidermal surface with stomate and papillae; 45: T. S. of leaf showing both surfaces).

high overarching group around stomata. Stomata: Class 5. Hypodermis: 3-layered on both surfaces. Rhomboidal crystals few in palisade layers, around and in VB's and in mesophyll. Mesophyll palisade with adaxial layer 3 times the depth of abaxial layers. Copious amount of raphide sacs in both palisade layers, also in innermost hypodermal layers. Fibres in groups of 2-3 in palisade.

Comments: The large fibrous strands of *P. pectinatus* are very notable. In *P. danckelmannianus* the very numerous raphide sacs are particularly noticeable. The papillosoity of *P. gibbsianus* is very marked. Thus these species stand apart. It is appropriate that they are thus relegated to different subsections of Sect. Acrostigma. *P. pectinatus* in Subsect. Papilionati, *P. danckelmannianus* in Subsect. Dimissistyli, and *P. gibbsianus* in Subsect. Scabridi.



Figs. 46-50. 46-47: *Pandanus danckelmannianus* (46: T.S. of stomate and dendritic papillae; 47: epidermal surface with stomate and papillae), 48-50: *P. platystigma* (48: T.S. of stomate with long dendritic papillae; 49: epidermal surface; 50: T.S. showing part of adaxial epidermis, hypodermis, some unligified fibres and chlorenchyma).

Sect. Pseudacrostigma B. C. Stone

P. platystigma Martelli. (Figs. 48-50)

Costal-intercostal differentiation distinct. Costal regions with cells having sinuous anticlinal walls and non-papillose. Intercostal cells are papillose. Papillae dendritic, 1-2 per cell, forming tall columnar "stockade" surrounding and overarching stomata. Stomata: Class 5. Hypodermis: 2-layered on both surface. Rhomboidal crystals very few in hypodermis and mesophyll, absent around VB's. Mesophyll palisade with many fibre strands,

each of 1-6 fibres.

Comments: The sinuous anticlinal walls and elaborate stomata are striking features of this species, hence of this section. *P. eydouxia* shows similar characters but is distinguished by having rhomboidal crystals around and in the VB's and a much more multiseriate hypodermis.

Conclusions

- (1) Lack of unligified fibres and abundance of raphides reaffirm the status of *P. danckelmannianus* in Subsect. Dimissistyli.
- (2) Abundance of fibres and lack of raphides confirm distinct subsectional status of *P. gibbsianus* (Subsect. Scabridi).
- (3) *P. matthewsii* shows close anatomical similarity to *P. pentodon*; both are in Sect. Asterostigma.
- (4) *P. fragrans* (Pandanus) is anatomically different from both *P. kaida* (Pandanus) and *P. kirkee* (Pandanus).
- (5) *P. ambongensis* and *P. myriocarpus* (Sect. Heterostigma) are very similar anatomically.
- (6) Distinctness of Subsect. Multispina within Sect. Rykia is demonstrated at the anatomical level by study of *P. multifurcatus*.
- (7) Pitted walls of hypodermal cells have been observed in *P. clarkei* and *P. gibbsianus*. They are not closely related species.
- (8) Two types of rhomboidal crystals have been observed, one type with smooth, plain faces (more common), another type with a striated face (seen in Sect. Maysops).
- (9) Unusual abundance of rhomboidal crystals is noticeable in a second species, *P. clementis*, in Sect. Jeanneretia.
- (10) Rhomboidal crystals are rare or even absent in Sect. Acrostigma.
- (11) Sect. Eydouxia (*P. eydouxia*) in anatomical features resembles some spp. of Sect. Pandanus.
- (12) Outstandingly characteristic species are *P. pectinatus*, *P. simplex*, *P. spinistigmaticus*, *P. clementis*, and *P. gibbsianus*.
- (13) Occurrence of stomata within "stockades" of papillae is observed in *P. simplex*.
- (14) Correlation of anatomical features with environmental factors continues to be problematical or even impossible.

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References

- Kam, Y.K. 1969. Comparative systematic foliar anatomy of Malayan *Pandanus*. M. Sc. Thesis, Univ. of Malaya Library. — 1971. Morphological studies in Pandanaceae III. Comparative systematic foliar anatomy of Malayan *Pandanus*. Bot. J. Linn. Soc. 64(4): 315-351. — and B.C. Stone. 1970. Morphological studies in Pandanaceae IV. Stomate structure in some Mascarene and Madagascar *Pandanus* and its meaning for infra-generic taxonomy. *Adansonia* n. s. 2, 10(2): 219-246. Tomlinson, P.B. 1965. A study of stomatal structure in Pandanaceae. *Pacif. Sci.* 19(1): 38-54.

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解剖学的特徴をタコノキ科の分類に利用しようとする研究の一環として、タコノキ属の23種についての研究結果を報告した。本属では注意して使えば、外部形態による分類に対して、解剖学的特徴は補足的な意義づけを与えることが確認され、また属内の類縁関係を評価するためにも役立つことが判明した。さらに時には解剖学的特徴によって種を同定することも可能である。

□Dombremez, J. F., F. Vigny & L. H. J. Williams: **Bibliographie du Népal** Vol. 3 Sciences Naturelles, Tom. 2 Botanique 126 pp. 1972. Centre National de la Recherche Scientifique, Paris. 40. 90 F.F. フランスで企画されたネパールに関する文献集の植物編が出版された。ネパールに重点があるが、かなり広くヒマラヤ全般にわたる文献が採録されており、第3部に植物に関する732項目の文献が著者のABC順に紹介されている。しかし本書の特色はネパールの植物に関連のある文献以外の情報が色々集められていることである。第1部は序論、第2部にはネパールにある植物関係の研究所や大学と職員の名もあげられており、第4部では約20の大事項別に文献がまとめて解説してある。第5部にはヒマラヤ産植物の標本を所蔵している世界のハーバリウムのリストがあり、第6部にはヒマラヤ植物を栽植している植物園、第7部にはネパールでの植物採集者のリストがあって、主要な採集旅行が地図で示されていて仲々便利である。本文はフランス語で書かれているが大部分に英訳がつけられているのも親切である。 (原 寛)