The Morphology and Systematics of *Pandanus* Today (Pandanaceae)*

by

BENJAMIN C. STONE

Department of Botany, University of Malaya, Kuala Lumpur, Malaysia

Summary

More than 500 species of *Pandanus* are now known, and 70% of these have been described since 1900, nearly half since 1939, and new ones are being discovered. Many obstacles have prevented the completion of a monograph (dioecism, large structures, remote locales) but perhaps the most serious has been ignorance of morphology and morphogenesis. Studies of these are thus of critical importance. Micromorphological-anatomical data and cytotaxonomic data have recently become available, permitting data integration not previously possible. This has resulted in a new detailed infrageneric classification which can contribute to understanding of the phylogeny. This classification recognizes 8 subgenera, 62 sections, and 22 subsections covering 468 species and numerous synonyms. Chromosome numbers are 2n = 60 (1 species of *Pandanus, P. spiralis* R. Br., has 2n = c. 120). Remarkable stomate variability is tied almost exclusively to systematic relationship.

I. Introduction

The Pandanaceae is a family now generally conceded to be the sole member of the Order Pandanales (Monocotyledonae). The Typhaceae and Sparganiaceae (formerly included) are not closely related to Pandanaceae and form a distinct Order Typhales.

Although known to botanists for some three centuries, the Pandanaceae accounted for in Warburg's Monograph (1900) were 180 species of *Pandanus*, about fifty spp. of *Freycinetia*, and one of *Sararanga*. No further genera have been discovered but the number of known species has grown and there are about 700 binomials currently. The foremost students of the family since 1900 have been Martelli, Merrill, Pichi-Sermolli, and St. John. More vigorous exploration in the Palaeotropics has vastly increased the available study material; much fieldwork has significantly augmented the herbarium study.

But many problems remain which impede full understanding of the family, in particular the largest genus *Pandanus*. With over 500 species, *Pandanus* posed severe difficulties in establishing interspecific relationships and an infrageneric classification.

II. Traditional taxonomic characters and unresolved problems

The salient features of previous taxonomic work on *Pandanus* was the virtually complete dependency on the characters of the ripe fruits. Nearly all described species and infrageneric taxa were based on fruit-characters. Since all the plants are dioecious, this resulted in almost sure ignorance of the males. Staminate specimens could seldom be identified. The problem was brought about by the

---

* Based on a paper read at the International Botanical Congress at Leningrad, 1975 (Abstract in [A. Takhtajan (Ed.),] *Abstracts of the papers presented at the XII International Botanical Congress July 3–10, 1975* (I):100).

rarity of good staminate material in herbaria (in turn the result of the ephemeral nature of the male flowers in nature), and the difficulty of correlating staminate and pistillate specimens both in the field and in the herbarium. Sterile material was impossible to identify.

Clearly, a taxonomic system which relied entirely on fruit characters, in a genus of strictly dioecious plants, was inadequate both for practical identification and for studies of phylogeny. For the purposes of most botanists, identification of *Pandanus* was either uncertain or impossible.

In view of this situation it was obviously desirable to seek taxonomic characters which were shared by both staminate and pistillate plants, i.e. vegetative characters, including those revealed by micromorphology and anatomy. During the past two decades our efforts have been turned to solutions to the problems described. The main features of the work, carried out by various persons at several institutions, are described below.

III. New Investigations and their Results

A. Gross Morphology. — In general three main aspects have been developed: (1) Fuller quantification of characters, particularly of vegetative structures. Example: the mainly qualitative descriptions of leaves have been replaced by analyses giving data such as tooth (prickle) size and spacing, vein number, variation in leaf length and width, etc. (2) The discovery and correlation of staminate with the pistillate-plants of the same species, and full descriptions and taxonomic use of staminate characters. Example: field work yielding field knowledge of population structure, phenology, breeding behaviour, and ecological distribution, has often led to correct correlation of sexes. Pollen characters have been studied only to a limited extent but may throw some light on species relationships, as has been demonstrated in a few cases (e.g. *Pandanus sigmoideus* St. John). (3) Habit and morphogenetic field characters supplementing the existing herbarium knowledge, made possible by augmented collection techniques, photography, field analysis of individuals in various growth stages, etc.

B. Morphogenesis and architecture (habit). – Work in this field has revealed the changes which occur in ontogeny from seedling to adult and has necessitated the recognition of 'juvenile' states which may differ radically from adult states, even in the same species. Progressive changes in anatomical features are correlated with the external changes in size and form, and indicate that anatomical characters must be derived from adult structures for reliable use in taxonomy and classification. Habit classification has become possible through the analysis of growth phases and it is now clear that adult form can be a major taxonomic character. This is especially clear in the case of *Pandanus* Sect. *Acanthostyla*, of Madagascar, a group of species which share the 'coniferoid' habit. Further studies of habit have been carried out by Guillaumet (1973), based on the more general work of Hallé and Oldemann (1970; 1975). The 'lateral' inflorescences of Sect. *Cauliflora* and Sect. *Tridens* are similar examples of habit specialization which offer taxonomic utility.

C. Anatomy. — Anatomical studies of *Pandanus* date back at least as far as Solla (1887) but their significance in relation to taxonomy was not appreciated. With resumption of such studies by Tomlinson (1965), Kam (1969), Gineis (1969), and now especially by K. L. Huynh (1974), the correlation between anatomical features and other characters became clear. It is now evident that, in general, anatomical characters form a fairly reliable basis for the discrimination of species-groups, and furthermore, it has become clear that these species-groups usually correspond to sections. Occasionally, single species stand out on anatomical grounds, and there are some cases in which anatomy seems not to offer clear support to sectional discrimination, but in a great majority of cases the anatomical data has had a beneficial and significant effect on infrageneric taxonomy. The anatomical characters used have been chiefly from the leaves, and as demonstrated by Kam, only fully adult organs could be compared. Within these limits the appearance of particular anatomical features seems sufficiently constant and in rare cases may be diagnostic.

The tissues which furnish the characters are especially the epidermis, the stomatal complex, the hypodermis, the crystal cells, the chlorenchymatous layers, the fibrous strands and the vascular bundles. In particular, the range of variation in the epidermal tissues (including the stomata) proves to be of very great value. In order to rationalize the variation found, Tomlinson founded a classification of stomatal types, based on progressive complexity. This system was used by Kam and others and shown to correlate well with sectional taxa. More recently (1974) the classification has been refined by Huynh, who defines seven stomatal types and in turn finds a remarkably good correspondence with the infrageneric classification being developed by Stone. In fact, the anatomical data became the test by which the infrageneric taxa could be evaluated; where serious disharmony in anatomical features was revealed within a section, it was usually found to indicate an artificial classification which could be remedied by remodeling the Section e.g. by dividing it, or by reassigning some of its supposed component species to other sections. The anatomical data thus often revealed a 'hidden' flaw in previous taxonomic systems.

Examples of the variety of stomatal-complex structures revealed that all retain the basic tetracytic pattern but vary in relation to the production of elaborations, which are commonly in the form of papilliform protuberances arising from the cells of the stomatal complex and of the epidermis proper. The simplest arrangement is an essentially flat epidermis, the stomate flush with the surface, the epidermal cells merely forming a tessellate pattern. On adaxial surfaces of leaves the epidermis may be zoned or not; zonation involves differing cell shape and presence or absence of stomata in alternating bands corresponding to veins and inter-vein spaces. Such zonation produces a further character that may be used in addition to the stomatal type. Increasingly complex stomatal types develop as various cells produce papillae, and the entire epidermal surface or all the relevant zonal bands, may thus become papilliferous. The papillae themselves may be limited to one per cell, or may occur in sets on a cell: they may be of various simple forms or in more elaborate forms such as forked or dendritic. Papillae may form a stockade around the stomate, or around a group of stomata. The stomata may become considerably sunken below the general level of the epidermis.

The hypodermis may be of one or more cellular layers and may include crystal cells in various patterns and in various orientations. The crystals may be rhomboidal or occur as raphides; the former usually are more common in leaves, and may exist in two distinct forms, and in various sizes. The patterns of distribution of the crystal cells may be of some taxonomic value.

The chlorenchyma may be continuous or interrupted, and this distinction sometimes has a taxonomic significance.

The association of fibrous strands with particular tissues may also be constant enough for taxonomic use.

A considerable number of other anatomical features occur, some of which may on occasion have a taxonomic use, e.g. stomatal size and stomatal index, the occurrence of papillate stockades, etc.

Wherever data from anatomy conflicts considerably with a traditionally established taxonomic group it is likely that the latter is heterogenous and a re-evaluation of all the constituent species and their characteristics is in order. By application of this method the infrageneric classification can be established on a broader, firmer basis than otherwise possible. The concrete result of such application has been put forward as a new infrageneric scheme (Stone, 1974). In this system, eight subgenera are established (these are further grouped into four unnamed groups of 3, 2, 2 and 1 subgenera respectively). Each subgenus consists of one or more (up to sixteen) sections. Altogether, 62 sections are recognized. These in turn are in some cases divided into subsections. There are 468 species accounted for, i.e. probably 90% of the total (the remainder are excluded temporarily as either probable synonyms or because data is quite insufficient for placement).

D. Cytology. — The predominant chromosome number found in *Pandanus* is 60 (somatic): but one tetraploid (*P. spiralis* R. Br.) is known. However, only some 30 species have been 'counted'. The foremost workers in this field have been Tjio, Harada, Cheah (1969) and the work is being continued by Jong. The only discovery of some taxonomic significance is that in some cultivars (e.g. *P. spurius* Miq.) some cells at least may be aneuploid (with such numbers as 59 or 61 chromosomes). So far however, there is no significant input from chromosome studies, but the work has probably not progressed far enough to be sure that this will remain true. It is at least potentially interesting that the one case of tetraploidy occurs at the margin of the generic distribution (Northern Territory, Australia) where it seems to be the case that habitat and climatic conditions are marginal. The karyotype analysis by Cheah shows that the chromosomes are very small. There may be 0-4 pairs of SAT-chromosomes, and many are short rods which are hardly discriminable.

E. Embryology. — *Pandanus* is peculiar in that the mature embryo sac in the few species so far studied, has a condition of supernumerary nuclei (over and above the usual eight): these nuclei, as was shown by Fagerlind (1940), migrate in from the surrounding tissue at a late stage. Recently this has been reconfirmed in two Malayan species (Cheah and Stone, 1975). The other genera of the family do not appear to show this phenomenon. The significance, if any, to taxonomy, has yet to be discovered. However, circumstantial evidence for a few species indicates that reproduction may be apomictic: it is conceivable that this is related to the 'nuclear migration' as first noticed by Campbell and demonstrated by Fagerlind, but this remains to be investigated.

F. Palynology. — The pollen morphology has yet to be investigated in detail. Present evidence suggests that some variation exists and thus some taxonomic information may arise from studies of pollen. It is hoped to investigate this with the Scanning-Electron Microscope now available in the University of Malaya.

IV. Synopsis of the infrageneric taxa of Pandanus[1]

Group 1

Subgenus 1. *Rykia*

Sections:

(1) *Rykia* (with subsections Rykia, Bidens, Malaya, Multispina, Calcicola, Atrodentata, Gressittia)
(2) *Asterodontia*
(3) *Hombronia*
(4) *Mydiophylla*
(5) *Rykiopsis*
(6) *Solmsia*
(7) *Kaida*

Subgenus 2. *Lophostigma*

Sections:

(1) *Lophostigma*
(2) *Megastigma*
(3) *Karuka*
(4) *Maysops*
(5) *Metamaysops*
(6) *Paralophostigma*
(7) *Perrya*
(8) *Cauliflora*
(9) *Barrotia*
(10) *Liniobtutus*
(11) *Brongniartia*
(12) *Veillonia*
(13) *Bernardia*
(14) *Asterostigma*
(15) *Tridens*
(16) *Cheilostigma*

1. See Stone (1974) for bibliographic citations.

Subgenus 3. *Kurzia*

Sections:

(1) *Kurzia*
(2) *Microstigma*
(3) *Jeanneretia*
(4) *Pulvinistigma*
(5) *Curvifolia*
(6) *Involuta*
(7) *Marginata*
(8) *Cristata*
(9) *Kanehiraea*
(10) *Utilissima*

Group 2

Subgenus 4. *Vinsonia*

Sections:

(1) *Vinsonia*
(2) *Barklya*
(3) *Mammillarisia*
(4) *Dauphinensia*
(5) *Stephanostigma*
(6) *Heterostigma*
(7) *Souleyetia* with subsections Souleyetia and Sussea
(8) *Foullioya*
(9) *Acanthostyla*
(10) *Rykiella*
(11) *Lonchostigma*
(12) *Platyphylla*
(13) *Eydouxia*

Subgenus 5. *Martellidendron*

Sections:

(1) *Martellidendron*
(2) *Seychellea*

Group 3

Subgenus 6. *Pandanus*

Sections:

(1) *Pandanus*, with Subsections Pandanus, Austrokeura, and Insulanus
(2) *Fagerlindia*
(3) *Elmeria*
(4) *Athrostigma*
(5) *Intraobtutus*
(6) *Australibrassia*
(7) *Semikeura* with Subsections Semikeura and Elaphrocarpus
(8) *Excavata*
(9) *Megakeura*

Subgenus 7. *Coronata*

Sections:

(1) *Coronata*

Group 4

Subgenus 8. *Acrostigma*

Sections:

(1) *Acrostigma*, with Subsections Acrostigma, Scabridi, Dimissistyli, Ornati, Glaucophyllae, Parvi, Papilionati, Alticolae, and Pumili
(2) *Fusiforma*
(3) *Pseudacrostigma*
(4) *Epiphytica*

V. Future work needed.

A. Functional significance of micromorphological-anatomical characters: The great variation in anatomical structure which correlates so well with classification, seems so far to resist an ecological or physiological explanation. For example, the more elaborate stomatal types (five in Tomlinson's, six or seven in Huyhn's) suggest xeromorphy. Nonetheless, various species of *Pandanus* which are taxonomically unrelated and which have very different stomatal types, may occur sympatrically in exactly the same microhabitat, i.e. fresh-water swamps.

B. More precise developmental studies to determine the basis of different habit categories, as well as to provide a means to compare ontogeny in pandans with that in other plants.

C. Further cytological studies to determine if other examples of polyploidy exist, whether they correlate with classification and/or habitat, and whether they tend to cluster at the margin of the generic distribution as is apparently the case and would be expected theoretically on the basis of the evolutionary studies of e.g. Stebbins.

D. Palynological work as a basic survey and to correlate with taxonomy and with fossils, particularly to see whether palynomorphic form genera such as *Pandaniidites* can be in fact accepted as pandanaceous.

E. Distributional analysis as a partial basis of phylogenetic interpretation.

References

CHEAH, C. H. 1969. M.Sc. thesis, University of Malaya.

——— 1973. Chromosome studies of *Pandanus. Bot. Jahrb. Syst.* **93**: 498–529.

——— & B. C. STONE. 1975. Embryo sac and microsporangium development in Pandanus. *Phytomorphology* **25**: 228–238.

FAGERLIND, F. 1940. Stempelbau und Embryosackentwicklung bei einigen Pandanazeen. *Annls Jard. bot. Buitenz.* **49**: 55–78.

GINEIS, C. 1969. Étude anatomique de la plantule de *Pandanus* sp. *Bull. Inst. Fr. d'Afr. noir* **31 A,** 2: 325–339.

GUILLAUMET, J. -L. 1973. Formes et development des 'Pandanus' Malgaches. *Webbia* **28**: 495–519, 6 figs., 10 pls.

HALLÉ F. & R. A. A. OLDEMAN. 1970. *Essai sur l'architecture et la dynamique de croissance des arbres tropicaux.* Masson & Co., Paris.

——— 1975. Essay on the Architecture and Growth Dynamics of Tropical Trees. English translation by B. C. Stone. University of Malaya Press, Kuala Lumpur.

HUYNH, K. -L. 1974. La morphologie microscopique de la feuille et la taxonomie du genre *Pandanus. Bot. Jahrb. Syst.* **94**: 190–256.

KAM, Y. K. 1969. M.Sc. thesis, University of Malaya.

——— 1971. Morphological studies in Pandanaceae III. Comparative systematic foliar anatomy of Malayan *Pandanus. Bot. J. Linn. Soc.* **64**: 315–351.

——— & B. C. STONE. 1970. Morphological studies in Pandanaceae IV. Stomate structure in some Mascarene and Madagascar Pandanus and its meaning for infrageneric taxonomy. *Adansonia n.s.* **10**: 214–246.

SOLLA, R. F. 1884. Contribuzione allo studio degli stomi delle *Pandanee. Nuovo G. bot. ital.* **16**: 172–182.

STONE, B. C. 1974. Towards an improved infrageneric classification in *Pandanus* (Pandanaceae). *Bot. Jahrb. Syst.* **94**: 459–540.

TOMLINSON, P. B. 1965. A study of stomatal structure in Pandanaceae. *Pacif. Sci.* **19**: 38–54.

WARBURG, O. 1900. Pandanaceae, in A. Engler, *Das Pflanzenreich, 3,* **IV.** 9: 1–97. Engelmann, Leipzig.