Proc. Indian natn. Sci. Acad. **B51** No. 5 pp 596-608 (1985)

Frequency of Stomata in Leaves of Young and Adult Palms

MONORANJAN GHOSE, B M JOHRI[1] and T A DAVIS[2]
Indian Statistical Institute, Calcutta 700035

(Received 5 August 1985)

A comparative study has been made with reference to frequency of stomata per unit area, their length on the abaxial and adaxial epidermis, width of individual epidermal cells, and stomatal index between young and adult plants of ten species of palms: *Areca triandra, Caryota urens, Chrysalidocarpus lutescens, Hyphaene dichotoma, Livistona rotundifolia, Phoenix pusilla, P. reclinata, Roystonea regia, Salacca zalacca* and *Veitchia merrillii.* The stomatal index and the number of stomata per unit area increase significantly in most of the adult plants. The index value decreases in adult *Phoenix pusilla.* The length of guard cells decreases significantly in two adult plants with isolateral leaves, but increases in others. The width of epidermal cells decreases significantly in most of the palms except the arecoid major group. Negative associations exist between the stomatal frequency and the size (length) of stomata (in two plants), and between the stomatal frequency and the width of epidermal cells (in six plants). There is hardly any resemblance between the sequence of the species according to Moore's (1973) systematic classification of palms, and the sequence according to the frequency of stomata.

Key Words: Palms, Stomata, Leaves, Epidermal cells, Stomatal index

Introduction

The study of stomata in palms has received much attention. Most of the work is confined to the leaves of adult palms (Tomlinson 1961, Bavappa 1966, Mahabale 1982, Mahabale & Shirke 1967, Trivedi & Upadhyay 1979). There is however, very little work on young palms (Ghose & Davis 1973, Basu & Basu 1978). The present article is an extension of a previous work (Ghose & Davis 1973) where it has been shown that significant differences in epidermal characters between young and adult palms exist. Therefore, the objective of the present article is (*a*) to confirm the earlier findings, and (*b*) to find out the range of variations between young and adult plants in respect to stomatal

[1]Department of Botany, University of Delhi, Delhi 110007
[2]J B S Haldane Research Centre, Nagercoil 4, Tamil Nadu

frequency, length of guard cells, stomatal index, and width of epidermal cells in ten different species of palms.

Materials and Methods

Epidermal peelings of lamina were prepared from seedlings, and adult forms of ten species of palms (table 1) according to the method described elsewhere (Ghose & Davis 1973). Most of the seedlings were raised from seeds collected from the Indian Botanic Garden, Howrah. The seeds of *Veitchia* were collected in Australia. Seeds were sown at different times according to their availability. The age of the seedlings ranged from 8 to 19 months. Some of the samples from adult specimens were collected from the Indian Botanic Garden, Howrah, and the garden of the Legislative Assembly, Calcutta, and the remaining from the premises of the Indian Statistical Institute.

In pinnate-leaved palms pieces of lamina were collected approximately half-way between the base and apex of a leaflet, inserted about half-way from the base to the apex of rachis. In palmate-leaved palms, or in seedling leaves which had not yet started splitting into leaflets, collections were in a region approximately half-way between the base and apex of a sector from one side of lamina. The species examined are tabulated according to Moore's (1973) classification of palms (table I). Of the ten species studied, *Hyphaene dichotoma*, *Phoenix pusilla* and *P. reclinata* have isolateral leaves and the rest dorsiventral.

Results

The mature stomata of palms are of the tetracytic type. Each stoma is surrounded by four subsidiary cells, two terminal or polar cells, and two lateral cells. Terminal subsidiary cells are short and wide, while lateral ones are long and narrow and lie parallel to guard cells. Each guard cell has two cutinized ledges. Guard cells in *Caryota urens* are provided with transverse cuticular striations (figure 1A).

Stomatal Frequency

The total number of stomata in a field (obtained by using a lens-combination of 7×40) was counted. The area of each field was calculated as 0.17 sq. mm. Ten different fields per sample were examined at random. The data presented in table 1 are the mean for one field covering 0.17 sq. mm. For all the species, figures relating to young as well as adult palms are given.

Table 1 shows that the number of stomata, per unit area, increases in adult plants. *Livistona rotundifolia* registers over 339%, *Phoenix reclinata* over 179%, and *Veitchia merrillii* (figure 1B, C) over 109% increase in the number of stomata on abaxial surface. Stomata are absent on the adaxial epidermis of young as well as adult *V. merrillii* (figure 1D). Stomatal distribution on both the surfaces is almost similar in *H. dichotoma*. The stomata are totally absent on the adaxial epidermis of adult palms, but in young palms they are present in small numbers in *Areca triandra* and *L. rotundifolia* (figure 2A). The adaxial epidermis contains scattered stomata in *C. urens* (figure 2B), *Chrysalidocarpus lutescens* (figure 2C), *L. rotundifolia* (figure 2A), *Roystonea regia*, and *Salacca zalacca*. In young plants of *P. pusilla* and *P. reclinata* (figures 2D, 3A) the adaxial frequency is slightly less-than-half that of abaxial. In adult *P. reclinata* the frequency is almost the same on both surfaces.

Length of Guard Cells

The length of guard cells shows an increasing trend as the palms grow (table 2), the exceptions are *Hyphaene dichotoma* (figures 3B, C) and *Phoenix reclinata*. Among young plants the guard cells are the longest

Table 1 *Stomatal frequency in palm leaves (per unit area of 0.17 sq. mm)**

Major groups and species	Young plants		Adult Plants	
	Abaxial epidermis	Adaxial epidermis	Abaxial epidermis	Adaxial epidermis
I. Coryphoid				
Livistona rotundifolia (Lam.) Mart. (10)	27.7±0.47	3.1±0.57	121.8±1.60	Nil
II. Phoenicoid				
Phoenix pusilla Gaertn. (16)	31.9±1.77	13.2±0.87	39.3±0.19	14.7±0.89
P. reclinata Jacq. (8)	27.3±2.26	11.9±1.82	76.3±2.05	73.2±1.75
III. Borassoid				
Hyphaene dichotoma (white) Furtado (15)	14.2±0.94	11.1±0.72	27.2±0.81	28.5±0.58
IV. Lepidocaryoid				
Salacca zalacca (Gaertn.) Yoss (12)	20.6±0.62	Occasional —	30.2±0.96	0.8±0.36
VI. Caryotoid				
Caryota urens L. (12)	9.9±0.46	1.6±0.34	17.1±1.00	1.9±0.38
XII. Arecoid				
Areca triandra Roxb. (19)	10.5±0.89	0.2±0.13	15.4±0.94	Nil
Chrysalidocarpus lutescens H.A. Wendl. (16)	25.2±1.02	1.2±0.88	46.5±2.20	0.9±0.90
Roystonea regia (H.B.K.) Cook (11)	19.0±0.67	1.5±0.48	35.6±0.76	0.5±0.34
Veitchia merrillii (Becc.) Moore (10)	14.1±0.93	Nil	29.6±1.22	Nil

The classification shown above is that of Moore (1973). The age of the plant in months is given in parentheses after the binomial

*Average for 10 observations

Table 2 *Length of guard cells (μm) in palm lamina**

Species	Young plants		Adult plants	
	Abaxial epidermis	Adaxial epidermis	Abaxial epidermis	Adaxial epidermis
Livistona rotundifolia	16.7±2.13	18.0±0.46	19.7±0.53	Nil
Phoenix pusilla	23.4±3.16	25.1±0.41	27.2±0.59	27.2±0.47
P. reclinata	22.1±0.40	22.6±0.50	18.6±0.28	19.4±0.38
Hyphaene dichotoma	39.7±0.50	38.0±0.66	37.1±0.81	36.9±0.63
Salacca zalacca	28.0±0.38	26.0±0.84	33.9±0.48	33.7±0.72
Caryota urens	37.4±2.97	38.5±0.38	41.4±0.76	43.9±0.40
Areca triandra	33.5±0.38	33.5±0.52	36.5±0.69	Nil
Chrysalidocarpus lutescens	22.6±0.50	23.1±0.53	27.0+0.60	26.7±0.58
Roystonea regia	30.5±0.48	29.9±1.83	37.3±3.43	33.3±0.38
Veitchia merrillii	26.7±1.23	Nil	33.6±0.65	Nil

*Average for 10 observations

in *H. dichotoma* (figure 3B), and shortest in *Livistona rotundifolia* (figure 2A). In adult plants the length of guard cells is maximal in *Caryota urens* (figure IA), and minimal in *P. reclinata*. The length of guard cells between abaxial and adaxial surfaces (when present) does not differ significantly, both in young and adult palms, except in adult *Roystonea regia*.

Stomatal Indices

The stomatal index was calculated from abaxial epidermis of both young and adult plants (table 3). Among the young plants, the lowest index value is in *L. rotundifolia*, and highest in *Salacca zalacca*. In adult plants the minimum value is in *Phoenix pusilla*, and maximum in *Roystonea regia*. The increase of index value from young plants to adult plants is highest in *L. rotundifolia* (477.66%), and lowest in *P. reclinata* (20.77%). It may be noted that, in almost all the species, the stomatal index is higher in adult plants except in *P. pusilla*. The per cent increase of index value for adult plants with isolateral leaves (i.e. *P. pusilla* and *P. reclinata*) is either negative or insignificant.

Width of Cells

The width of epidermal cells on both abaxial and adaxial epidermis has been compared in young and adult plants (table 4). The maximum width in both young and adult palms occurs in *S. zalacca* (figures 3D, 4A,B) followed by *Areca triandra* (figure 4C,D) and minimum in *L. rotundifolia* (figure 2A). The adaxial epidermal cells are often wider than abaxial cells in dorsiventral leaves : *Areca triandra* (figures 4D, 5A), *Caryota urens* (figures 1A, 2B), *Chrysalidocarpus lutescens* (figures 2C, 5B), *Roystonea regia* and *Salacca zalacca* (figures 3D, 4A). A few exceptions occur in the dorsiventral leaves of *L. rotundifolia* and *Veitchia merrillii* (figure 1C, D) where the adaxial epidermal cells are narrower than the abaxial cells. The situation is reverse in the plants with isolateral leaves, e.g. *H. dichotoma*, *P. pusilla* and *P. reclinata*.

The width of epidermal cells becomes significantly smaller in adult *Caryota urens* (figures 1A, 2B), *H. dichotoma* (figures 3B, C), *L. rotundifolia*, *P. pusilla* (figures 5C, D), *P. reclinata* and *S. zalacca* (figures 3D, 4B).

Table 5 shows the *t*-values of various observations and measurements, and their significance at the 1% and 5% levels with d.f. 18. From this table it appears that the differences of stomatal frequencies between adult and young plants on abaxial epidermis are highly significant at the 1% level, and on adaxial epidermis, out of the three species (with isolateral leaves) calculated, two are significant at the 1% level. The difference of length of guard cells between adult and young plants on abaxial epidermis are significant at the 1% level in five species, and at 5% level in one species, and on adaxial epidermis the *t*-values for five species are significant at 1% level. That is, for two species (with isolateral leaves) the *t*-values on both abaxial and adaxial epidermis are significantly negative which indicate that the length of guard cells decrease significantly in adult plants. The *t*-values of width of epidermal cells are significant at the 1% level in six species on abaxial and adaxial epidermis, and at 5% level in two species on abaxial epidermis. The significantly negative *t*-values occur in six species on abaxial epidermis, and five species on adaxial epidermis. These findings indicate that the width of epidermal cells decreases in adult plants.

Conclusions and Discussion

The number of stomata per unit area is significantly higher in adult than in young plants. In *Phoenix reclinata* the increase, especially on adaxial epidermis, is phenomenal. Plants with isolateral leaves (e.g. *Hyphaene dichotoma*,

Table 3 *Stomatal indices of young and adult palms (from abaxial epidermis)*

Species	Young plants (A)	Adult Plants (B)	B–A	% increase
Livistona rotundifolia	2.73	15.77	13.04	477.66
Phoenix pusilla	5.14	4.54	–0.60	–11.67
P. reclinata	5.20	6.28	1.08	20.77
Hyphaene dichotoma	5.81	8.24	2.43	41.82
Salacca zalacca	10.21	15.41	5.20	50.93
Caryota urens	5.07	8.67	3.60	71.01
Areca triandra	5.23	7.88	2.65	50.67
Chrysalidocarpus lutescens	7.88	10.16	2.28	28.93
Roystonea regia	8.31	17.03	8.72	104.93
Veitchia merrillii	6.84	11.69	4.85	70.91

Table 4 *Width of an epidermal cell (μm)**

Species	Young plants		Adult plants	
	Abaxial epidermis	Adaxial epidermis	Abaxial epidermis	Adaxial epidermis
Livistona rotundifolia	8.1±0.21	6.7±0.18	5.9±0.16	5.0±0.03
Phoenix pusilla	10.9±0.20	10.6±0.22	8.5±0.20	8.5±0.35
P. reclinata	10.1±0.31	10.0±0.55	6.3±0.28	6.7±0.24
Hyphaene dichotoma	15.4±0.41	15.0±0.37	11.7±0.52	11.3±0.36
Salacca zalacca	28.0±0.97	31.5±0.31	24.9±0.62	28.4±0.73
Caryota urens	16.5±0.38	17.0±0.65	14.5±0.08	15.9±0.39
Areca triandra	19.7±0.87	24.6±1.02	24.8±0.63	27.1±2.02
Chrysalidocarpus lutescens	14.2±0.27	16.5±0.28	13.7±0.27	16.1±0.84
Roystonea regia	12.7±0.44	14.6±0.25	14.2±0.30	16.7±0.51
Veitchia merrillii	21.9±0.52	18.7±0.51	22.0±0.97	18.3±0.93

* Average for 10 observations

Table 5 *Statistical evaluation of the variations of quantitative characteristics of stomata and epidermal cells between young and adult palms*

Species	Stomatal frequency				Length of guard cells				Width of epidermal cells			
	Abaxial epidermis		Adaxial epidermis		Abaxial epidermis		Adaxial epidermis		Abaxial epidermis		Adaxial epidermis	
		Statistical Significance		Statistical Significance		Statistical Significance		Statistical Significance		Statistical Significance		Statistical Significance
Livistona rotundifolia	56.428	++	—	—	1.367	—	—	—	—8.485	++	—9.097	++
Phoenix pusilla	4.157	++	1.205	—	1.170	—	3.340	++	—8.485	++	—5.177	++
P. reclinata	16.059	++	24.279	++	—7.004	++	—5.032	++	—9.073	++	—5.633	++
Hyphaene dichotoma	10.477	++	18.820	++	—2.689	+	—1.118	—	—5.527	++	—7.187	++
Salacca zalacca	8.400	++	—	—	9.637	++	6.960	++	—2.701	+	—3.871	++
Caryota urens	6.541	++	—	—	1.286	—	9.751	++	—5.099	++	—1.491	—
Areca triandra	3.785	++	—	—	3.796	++	—	—	4.739	++	1.131	—
Chrysalidocarpus lutescens	8.784	++	—	—	5.698	++	4.569	++	1.152	—	—0.440	—
Roystonea regia	16.384	++	—	—	1.955	—	1.867	—	2.704		3.680	++
Veitchia merrillii	10.104	++	—	—	4.974	++	—	—	0.091	—	—0.453	—

The evaluation of *t*: + significant ($P=0.05$); ++ significant ($P=0.01$)

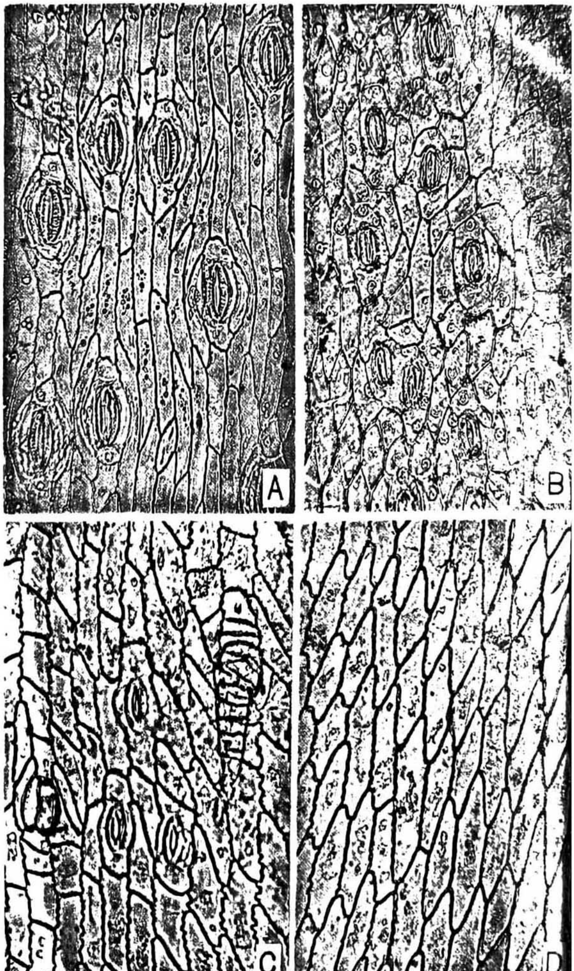

Figure 1 A–D Epidermis of lamina, surface view (× 330); **A**, *Caryota urens*, abaxial epidermis of adult plant; **B**, *Veitchia merrillii*, abaxial epidermis of adult plant; **C**, *V. merrillii*, abaxial epidermis of young plant; **D**, *V. merrillii*, adaxial epidermis of young plant

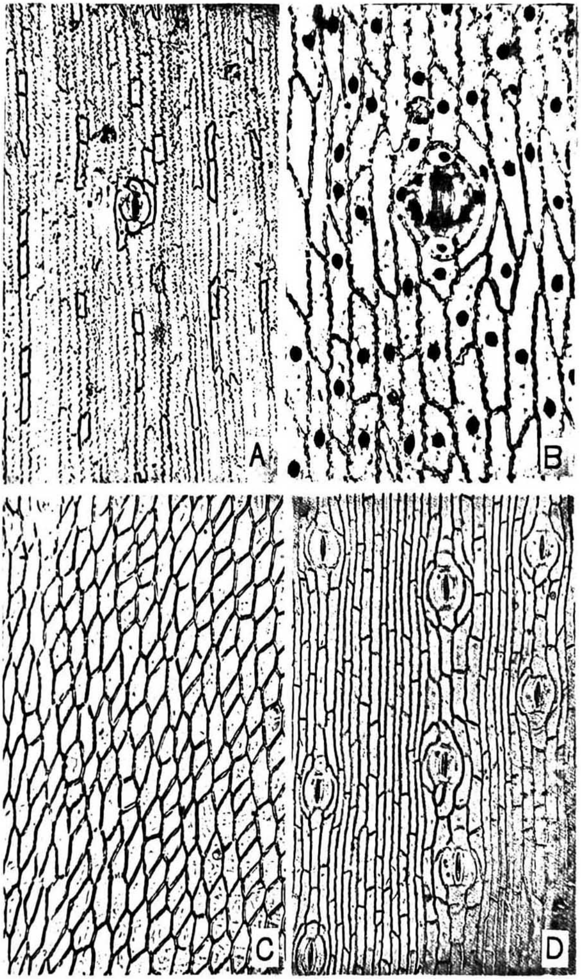

Figure 2 A-D Epidermis of lamina, surface view (× 330); **A**, *Livistona rotundifolia*, adaxial epidermis of young plant; **B**, *Caryota urens*, adaxial epidermis of young plant; **C**, *Chrysalidocarpus lutescens*, adaxial epidermis of adult plant showing a stoma on left side top of the photomicrograph; **D**, *Phoenix reclinata*, abaxial epidermis of young plant

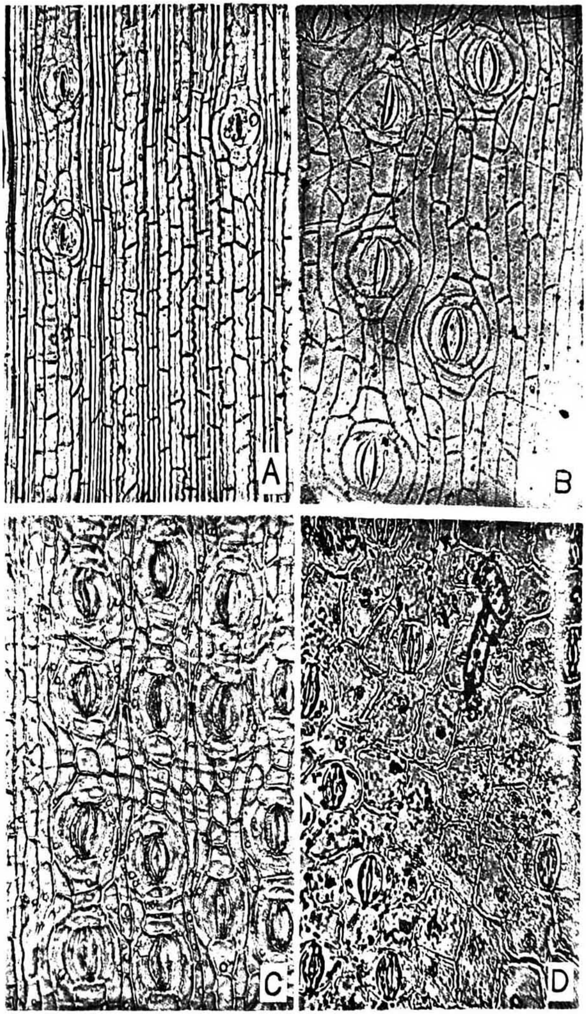

Figure 3 A–D Epidermis of lamina, surface view (× 330); A, *Phoenix reclinata*, adaxial epidermis of young plant; B, *Hyphaene dichotoma*, adaxial epidermis of young plant; C, *H. dichotoma*, adaxial epidermis of adult plant; D, *Salacca zalacca*, abaxial epidermis of young plant

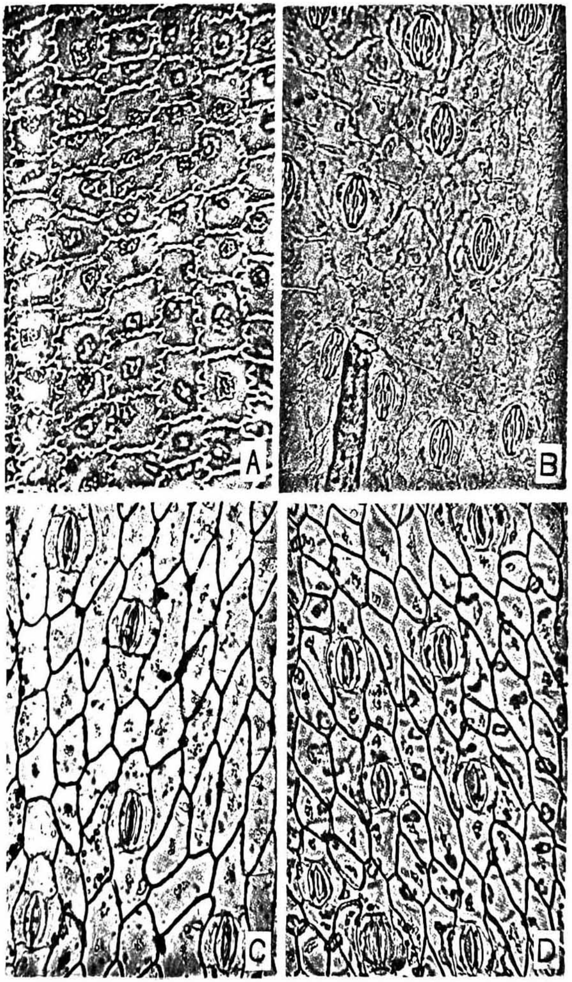

Figure 4 A-D Epidermis of lamina, surface view (× 330); A, *Salacca zalacca*, adaxial epidermis of young plant; B, *S. zalacca*, abaxial epidermis of adult plant; C, *Areca triandra*, abaxial epidermis of young plant; D, *A. triandra*, abaxial epidermis of adult plant

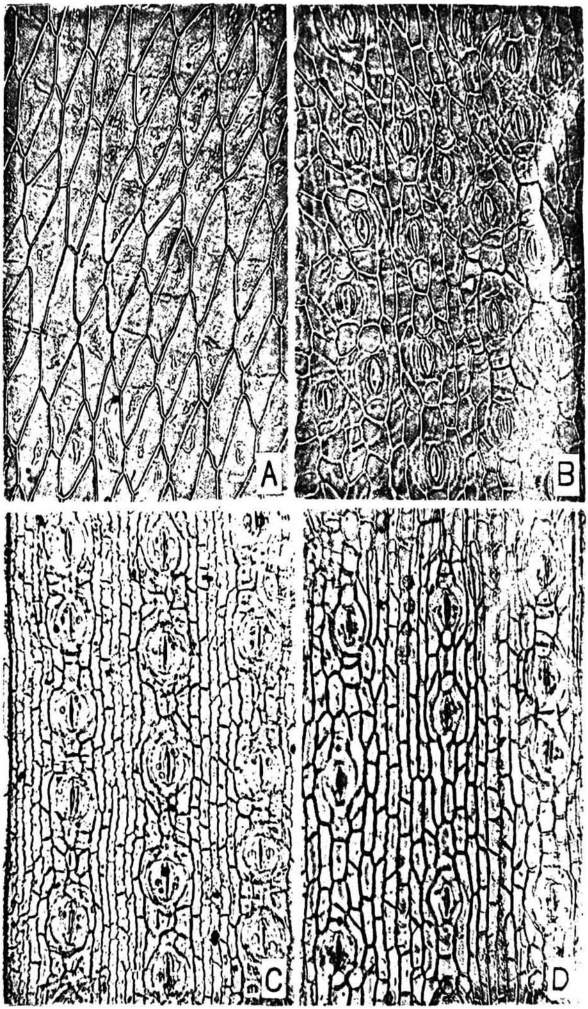

Figure 5 A–D Epidermis of lamina, surface view (× 330); A, *Areca triandra*, adaxial epidermis of adult plant; B, *Chrysalidocarpus lutescens*, abaxial epidermis of adult plant; C, *Phoenix pusilla*, abaxial epidermis of adult plant; D, *P. pusilla*, abaxial epidermis of young plant

Phoenix pusilla and *P. reclinata*) show almost equal or considerable number of stomata on abaxial and adaxial epidermis. On the other hand, plants with dorsiventral leaves (e.g. *Areca*, *Caryota*, *Chrysalidocarpus*, etc.) occasionally have stomata on the adaxial surface. This finding is in conformity with the previous work of Ghose & Davis (1973) on different species of palms. In *Livistona rotundifolia* the frequency of stomata increases several-fold from young to adult plants which indicates that mass transformation of epidermal cells into guard cells takes place at a later stage of growth. A similar situation was also reported in *Livistona chinensis* by Ghose and Davis (1973).

It is evident from tables 1 and 5 that there are two negative associations: (*a*) between the stomatal frequency and the size (length) of stomata (e.g. *Phoenix reclinata* and *Hyphaene dichotoma*), and (*b*) between the stomatal frequency and the width of epidermal cells (e.g. *Livistona*, *Phoenix pusilla*, *P. reclinata*, *Hyphaene*, *Salacca* and *Caryota*). In other plants, particularly in the arecoid major group, these negative associations do not occur. Negative linear correlation between the frequency and length of guard cells have been reported by Kutik (1973), Salisbury (1927), Slavik (1963), Miskin and Rasmusson (1970), and others. Similarly, the negative linear correlation between the frequency of stomata and the area of epidermal cells were reported by Kutik (1973), Pazourek (1965), Salisbury (1927), and others. These correlations resulted from their investigations only in adult members of different taxa other than the palms.

The stomatal index varies significantly in the young and adult plants with dorsiventral leaves, and the variation is insignificant or negative in those with isolateral leaves. The width of epidermal cells also decreases significantly in adult plants. As the width of cells decreases in adult plants, the number of cells per unit area increases, and this increase might be more in plants with isolateral leaves than the concomitant increase in the number of stomata which lowers the index value.

The sequence of stomatal frequency in table 1 can be compared with the sequence of species according to Moore's (1973) classification of palms. The lowest frequencies (in adult plants) occur in species of arecoid and caryotoid groups, while the highest frequencies occur in species of coryphoid and phoenicoid groups. There is insignificant resemblance between Moore's (1973) systematic sequence of evolutionary lines and major groups, and the sequence based on stomatal frequency. There is considerable variation among the species of individual major groups in frequency of stomata. For example, within the arecoid major group, *Chrysalidocarpus lutescens* shows the highest frequency, and *Areca triandra* the lowest. Similarly, within the phoenicoid major group, the highest frequency occurs in *Phoenix reclinata* and lowest in *P. pusilla*.

References

Basu S K and Basu S 1978 Epidermal studies in eophylls (juvenile leaves) of some arecoid palms; *Bull. Bot. Sur. India* **20** 124–132

Bavappa K V A 1966 Morphological and anatomical studies in *Areca catechu* Linn. and *A. triandra* Roxb; *Phytomorphology* **16** 436–443

Ghose M and Davis T A 1973 Stomata and trichomes in leaves of young and adult palms; *Phytomorphology* **23** 216–229

Kutik J 1973 The relationships between quantitative characteristics of stomata and epidermal cells of leaf epidermis; *Biol. Plant.* **15** 324–328

Mahabale T S 1982 *Palms of India* (Pune: Maharashtra Association for the Cultivation of Science, Research Institute)

—— and Shirke N 1967 The genus *Caryota* in India; *J. Bombay nat. Hist. Soc.* **64** 462–487

Miskin K E and Rasmusson D C 1970 Frequency and distribution of stomata in barley; *Crop. Sci.* **10** 575–578

Moore Jr H E 1973 The major groups of palms and their distribution; *Gentes Herb.* **11** 27–141

Pazourek J 1965 The symmetry of the lateral leaflets of *Medicago sativa* L.; *Biol. Plant.* **7** 261–269

Salisbury E J 1927 On the causes and ecological significance of stomatal frequency with special reference to the woodland flora; *Phyl. Trans. R. Soc. Ser.* B **216** 1–65

Slavik B 1963 The distribution of transpiration rate, water saturation deficit, stomata number and size, photosynthetic and respiration rate in the area of the tobacco leaf blade; *Biol. Plant.* **5** 143–153

Tomlinson P B 1961 *Anatomy of the Monocotyledons.* Vol. II *Palmae* (London: Oxford University Press)

Trivedi B S and Upadhyay N 1979 Epidermal structures in Palmae; *Biol. Mem.* **4** 85–117