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Taxonomic significance of epidermal morphology in Nigerian Rhizophoraceae

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SUMMARY

Epidermal morphology of adaxial and abaxial leaf surfaces of five genera of the family Rhizophoraceae in Nigeria were studied by light microscopy. The epidermises are composed of variously shaped cells which, in surface view, range in outline from triangular, rectangular to more commonly hexagonal, polygonal and irregular. Cuticular striations are absent except in *Poga oleosa* in which conspicuous striae encircle the guard cells and run parallel to the axis of non-specialized epidermal cells. Anticlinal walls are either straight, curved or undulate. Leaves of all genera are hypostomatic. Paracytic stromata occur in *Cassipourea* and *Anisophyllea* while all species of *Rhizophora* possess cyclocytic stomata. The stomata of *Anopyxis* are of the anisocytic type and those of *Poga* anomocytic. The morphology of the guard cells and stomatal ledges varies significantly within the family. Evidence is produced to support the suspected hybrid nature of *Rhizophora harrisonii*. Other features of the epidermis that show variation include stomatal size, shape and density, size and density of epidermal cells, and cell wall thickness. Epidermal characters are of some utility in elucidating relationships and identifying some taxa within the family.

Key-words: Rhizophoraceae, epidermal morphology, taxonomy, Nigeria.

INTRODUCTION

Rhizophoraceae (*sensu lato*) is a small pantropical family of about 16 genera and 120 species of shrubs, climbers and trees (Melchior 1964; Tomlinson 1986). Four of these genera constitute the chief component of mangrove swamps around tropical shores and estuaries. The species of these mangrove plants usually possess several peculiar morphological and physiological attributes which are of considerable scientific interest and have therefore attracted the attention of many scientists. Some of the taxonomic historical accounts of the Rhizophoraceae have been given by Metcalfe & Chalk (1950), Hou (1958), Van Vliet (1976), Dahlgren (1988), and Juncosa & Tomlinson (1988) among others. The family was grouped into two separate subdivisions, viz: Rhizophoreae and Legnotideae, which were later elevated to family ranks (Blume 1849). A couple of years later, Bentham & Hooker (1865) maintained these two groups as tribes and added a third one, Anisophylleae, which consisted of two inland genera, *Anisophyllea* and *Combretocarpus*.

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On the basis of wood anatomical features, Marco (1935) separated the species of the family into three groups. He recognized the Rhizophoreae as a natural group with well-defined characteristics while splitting Legnotideae *sensu* Bentham & Hooker into two, viz: Gynotrocheae and Macarisieae, and lumping Anisophylleae with the Gynotrocheae. *Poga* and *Pellacalyx* were left unclassified because their features did not fit into either of the two categories. Metcalfe & Chalk (1950) confirmed the scheme proposed by Marco (1935) but doubted the distinctness of Gynotrocheae and Macarisieae. *Anopyxis* and *Sterigmapetalum*, which were placed provisionally in the Macarisieae, are found to fit reasonably well in this group while *Poga* Pierre and *Pellacalyx* Korth., which do not fit into any group, share many characteristics in common with other genera in this family (Metcalfe & Chalk 1950).

In the past few years, there has been increasing evidence for the segregation of the tribe Anisophylleae as a separate family (Cronquist 1983; Dahlgren 1983; Raven 1984). This is contrary to the earlier findings of Van Vliet (1976), who concluded that wood-anatomical data provided no convincing case for excluding the Anisophylleae, and the conclusions of Keating & Randrianasolo (1988) who could not separate the Anisophylleae from the Rhizophoraceae using new data from leaf structure.

Five genera of the family, viz: *Anisophyllea* R. Br. ex Sabine, *Poga* Pierre, *Cassipourea* Aubl.-Alston, *Rhizophora* L. and *Anopyxis* Engl., are found mostly in the lowland rain-forest belt of Nigeria (Hutchinson & Dalziel 1954). Some species of these genera have edible fruits while others are of varied use in African traditional medicine (Dalziel 1937). Apart from the timbers derived from the family, the tanniniferous bark of *Rhizophora* and a few other genera constitutes one of the most important economic products (Metcalfe & Chalk 1950). The genus *Rhizophora* which consists of three species in Nigeria, viz: *R. racemosa* G. F. W. Meyer, *R. harrisonii* Leechman and *R. mangle* L., is an important constituent of estuary mangrove forest which is very extensive in the delta regions of the River Niger. These three species have been studied ecologically by Savory (1953) and taxonomically by Keay (1953) who described them as distinct species. The taxonomic status of *R. harrisonii* has, however, been a subject of controversy. The work of Breteler (1969, 1977) revealed that this taxon is morphologically and ecologically intermediate between the two other species and its geographical distribution closely linked with both taxa. Breteler (1969), therefore, regarded *R. harrisonii* as a hybrid, *R. racemosa* and *R. mangle* being its parents. In a very recent floristic account of these five genera in Nigeria, Keay (1989) separated *Anisophyllea* and *Poga* from the other three genera and placed them in a new family, Anisophylleaceae, in accordance with the current trend in the taxonomy of the group.

The present study was undertaken to provide additional information on epidermal morphology in order to improve our understanding of species relationships, affinities, status and infrafamilial systematics of the Rhizophoraceae in Nigeria.

MATERIAL AND METHODS

Plant material used for this investigation was obtained from the Herbaria of the Forestry Research Institute of Nigeria, Ibadan (FHI), Royal Botanic Gardens, Kew (K), and Department of Biological Sciences, University of Lagos, Nigeria (LUH). Fresh specimens were also collected in the wild by the senior author and vouchers are deposited in LUH. Representative specimens of all taxa studied are cited below.

Genus: *Rhizophora* L.
R. racemosa G. T. W. Meyer: Calabar, *Binuyo & Wilcox* (FHI 454539); Benin, *Charter & Campbell* (FHI 43254); Calabar, *Daramola, Macauley & Oguntayo* (FHI 90342); Brass, *Gbile & Daramola* (FHI 93047); Ikorodu, *Okafor Macauley* (FHI 585667); Port Harcourt, *Gbile & Daramola* (FHI 93053); Ikorodu North, *Onochie* (FHI 26669); Lagos, *Olowokudejo 91* (LUH); Degema Creek, *Adebusyi* (FHI 58674), Bonny, *Olowokudejo & Ola 313* (LUH); Bakana, *Olowokudejo 526* (LUH) (10 specimens).
R. harrisonii Leechman: Nembe-Delta, *Marsh* (FHI 54694); Brass, *Daramola & Miller*; Warri, *Daramola & Miller* (FHI 47268). Degema, *Okafor* (FHI 60314); Lagos, *Savory* (FHI 36095) (5 specimens).
R. mangle L.: Lagos, *Savory* (FHI 36094); Lagos, *Onochie* (FHI 23310); Bonny, *Daramola* (FHI 43299); Degema, *Marsh* (FHI 57988), Dikki, *Olowokudejo 378* (LUH); Odeama, *Olowokudejo 609* (LUH) (5 specimens).

Genus *Cassipourea* Aubl.
C. congoensis R. Br. ex DC.: Bauchi, *Jackson* (FHI 17693); Kabba, *Daramola* (FHI 36943); Abeokuta, *Jones, Keay & Onochie* (FHI 14181); Ilaro, *Obaseki & Otaru* (FHI 27918); Ikorodu, *Gbile, Daramola & Ekwuno* (FHI 64022); Obudu, *Latilo* (FHI 30948); Jos, *Jackson* (FHI 14964); Onitsha, *Jones* (FHI 5026) (8 specimens).
C. eketensis Bak.f.: Eket, *Lawanson 133* (LUH); Eket, *Talbot 3213* (K) (2 specimens).
C. barteri (Hook.f.) N.E. Br.: Jalingo, *Abah* (FHI 32695); Benin, *Keay* (FHI 37734); Benin-Sapoba, *Onochie* (FHI 27687); Benin-Okomu, *Onochie* (FHI 13076); Benin, *Emwiogbon* (FHI 61736); Lagos, *Lancaster* (FHI 48383); Degema, *Osain* (FHI 60607); Brass, *Daramola* (FHI 46935) (8 specimens).
C. gummiflua Tul.: Oban, *Talbot 1757* (K); Oban, *Samson 48* (LUH) (2 specimens).

Genus *Anopyxis* Engl.
A. klaineana (Pierre) Engl.: Benin, *Odukwe* (FHI 34720); Benin, *Okafor* (FHI 33062); Benin-Orhiuomwon, *Emwiogbon & Osanyinlusi* (FHI 82360); Benin, *Keay* (FHI 28105); Orlu-Imo, *Tuke 261* (FHI) (5 specimens).

Genus *Anisophyllea* R.Br. ex Sabine
A. sororia Pierre.: Calabar, *Onochie* (FHI 36199); Akampka, *Osain* (FHI 36212A) (2 specimens).
A. purpurascens Hutch. & Dalz.: Oban, *Samson 114* (LUH); Oban, *Talbot s.n.* (K) (2 specimens).

Genus *Poga* Pierre
P. oleosa Pierre: Ikom, *Rosevear* (FHI 2140); Ikom, *Onochie* (FHI 18739); Akampka, *Emwiogbon & Osanyinlusi* (FHI 82362); Calabar, *Onochie* (FHI 36436); Oban, *Onyeachusin & Latilo* (FHI 54024); Akampka, *Ariwaodo* (FHI 100486) (6 specimens).

Epidermal preparations

Small pieces of each leaf sample (*c.* 5–8 mm^2) taken from a standard central position, usually midway between the apex and base of the lamina, were soaked in concentrated trioxonitrate (V) acid in capped specimen bottles for about 30 min to 72 h, depending on the nature of the leaf. Specimens that were not well macerated within this period were transferred to a water bath at 60°C for 60 min. Abaxial and adaxial epidermises were then teased apart using fine forceps and dissecting needle. Any mesophyll tissue adhering to the membrane was cleared out in water by means of a camel hair brush. Each epidermal

Table 1. Some leaf epidermal characters of the family Rhizophoraceae

Genera and species	No. of cells mm^2: mean ± SE		Anticlinal cell wall pattern	Epidermal cell width: mean ± SE	
	Adaxial	Abaxial		Adaxial (μm)	Abaxial (μm)
Rhizophora					
racemosa	700 ± 6·93	658 ± 7·09	Straight	15·39 ± 0·41	13·91 ± 0·58
harrisonii	593 ± 5·14	584 ± 9·13	Straight	16·07 ± 0·38	14·0 ± 0·58
mangle	574 ± 6·22	550 ± 8·60	Straight	17·34 ± 0·52	16·99 ± 0·63
Cassipourea					
congoensis	483 ± 7·49	432 ± 8·82	Straight/curved	21·08 ± 0·54	19·74 ± 0·55
eketensis	478 ± 8·43	461 ± 5·54	Straight/curved	19·97 ± 0·67	16·59 ± 0·93
barteri	433 ± 4·81	304 ± 3·47	Straight/curved	25·0 ± 0·56	24·0 ± 0·73
gummiflua	404 ± 3·0	313 ± 6·55	Straight/curved	23·05 ± 1·03	20·95 ± 1·16
Anopyxis					
klaineana	386 ± 3·55	339 ± 4·49	Curved	22·91 ± 0·6	19·38 ± 1·18
Anisophyllea					
sororia	328 ± 5·28	324 ± 6·65	Undulate	18·57 ± 0·78	17·7 ± 1·55
purpurascens	348 ± 4·71	331 ± 5·24	Undulate	19·42 ± 0·69	16·83 ± 0·81
Poga					
oleosa	305 ± 3·42	288 ± 4·30	Straight/curved	26·82 ± 1·25	23·02 ± 2·25

Abbreviations: mm^{-2}, per millimetre squared; SE, standard error.

membrane was transferred into 50% ethyl alcohol for 2 min to harden and then stained in safranin for 5 min before dehydrating in ethyl alcohol series. Each membrane was mounted in Canada balsam.

Photomicrographs were taken using a Zeiss 9901 Research Photomicroscope. One leaf sample per specimen was examined and the number of specimens studied in each species ranges from two to 10 as listed above, depending on the geographical distribution of the various taxa and the availability of specimens.

Fifty cells were selected randomly from each surface and measured by micrometer eyepiece. Fifty stomata were also measured at random from the abaxial surface. Descriptive statistics of means, standard deviations and standard errors were calculated for all variables.

RESULTS

Some of the observed epidermal characteristics of all species of Rhizophoraceae examined are summarized in Tables 1 and 2 where taxa are listed according to the classification of Hutchinson & Dalziel (1954) with a few nomenclatural adjustments. Representative photomicrographs depicting various micromorphological features of the adaxial and abaxial epidermises in each of the five genera are shown in Figs 1–3. Descriptive terminology is based on Stace (1965), Dilcher (1974) and Wilkinson (1979).

Adaxial and abaxial epidermises are composed of variously shaped cells which in surface view range in outline from triangular, rectangular to more commonly, hexagonal, polygonal and irregular. Two or more of these forms may occur within the same surface.

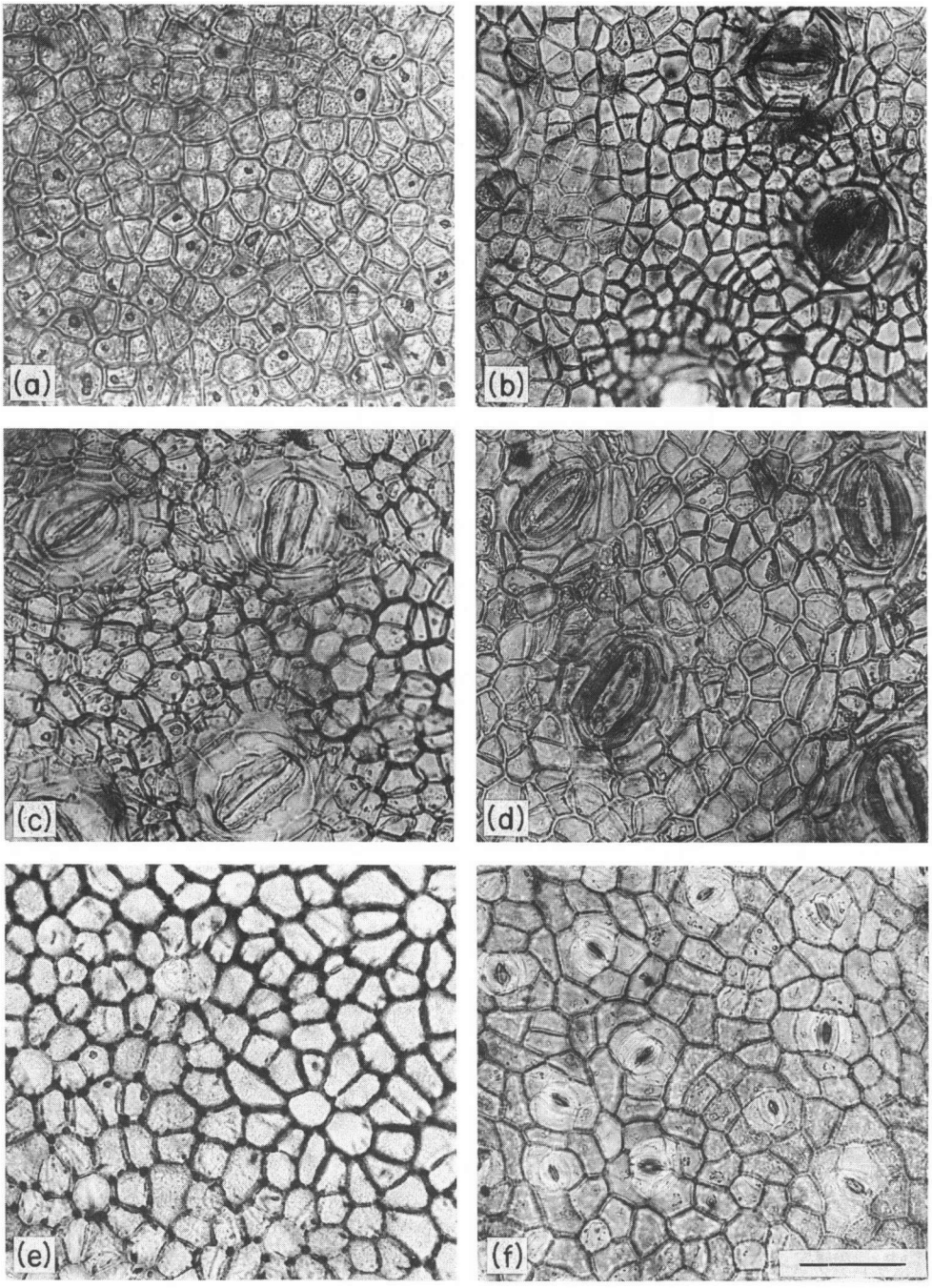

Fig. 1. Adaxial and abaxial epidermal surfaces of *Rhizophora* and *Cassipourea* species. (a) *Rhizophora racemosa*, adaxial epidermis. (b) *Rhizophora racemosa*, abaxial epidermis showing cyclocytic stomata and double stomatal rims. (c) *R. harrisonii*, abaxial epidermis showing cytocytic stomata. (d) *R. mangle*, abaxial epidermis. (e) *Cassipourea congoensis*, adaxial epidermis. (f) *C. congoensis*, abaxial epidermis showing paracytic stomata. All same scale = 50 μm.

The cells are generally thick-walled and, as a rule, those on the upper surface are slightly wider than those on the lower (Table 1) in each specimen. There are usually more cells per unit area on the adaxial than the abaxial side. *Rhizophora* species possess more cells per unit area, about 500–700, than all species of the remaining genera while the fewest cells, about 300, are found in *Poga oleosa*. Cuticular striations are absent from all genera except *Poga*, in which conspicuous striae generally encircle the guard cells and run parallel on the longest axis of the non-specialized cells (Fig. 3d). The striations on the adaxial surface are feeble and discontinuous resulting in a granular appearance (Fig. 3c). This surface also differs conspicuously from all other adaxial surfaces within the family by the occurrence of secondary anticlinal divisions of most of the cells as shown in Fig. 3c.

Anticlinal walls are usually straight in all species of *Rhizophora* (Fig. 1a–d), mostly slightly curved in *Anopyxis klaineana* (Fig. 2e, f) while a mixture of both straight and curved walls occur in species of *Cassipourea* (Figs 1e, f, 2a, b) and *Poga* (Fig. 3c, d). The two species of *Anisophyllea* examined are the only taxa with undulate walls (Fig. 3a, b) within the family.

Leaves of all species are hypostomatic. Stomata are dispersed randomly over the whole abaxial surface. The mean number of stomata per millimetre square varies from eight in *Rhizophora mangle* to 43 in *Cassipourea gummiflua* (Table 2). Paracytic stomata, in which the guard cells are accompanied on either side by one subsidiary cell parallel to the long axis of the pore and guard cells, occur in all species of *Cassipourea* (Figs 1f, 2b, d) and *Anisophyllea* (Fig. 3b). *Poga* has anomocytic stomata (Fig. 3d). In *Rhizophora*, four to eight subsidiary cells form a narrow ring around the guard cells, i.e. cyclocytic stomata, as in Fig. 1b for *R. racemosa*, Fig. 1c for *R. harrisonii* and Fig. 1d for *R. mangle*. The stomata of *Anopyxis klaineana* are of the anisocytic type, i.e. each stoma is surrounded by three cells, one of which is usually smaller than the other two (Fig. 2f). Most of the stomata from one leaf surface are more or less the same size but there is considerable variation among species and genera (Table 2). The largest stomata are those of *Rhizophora mangle* with a mean size of 41·63 × 12·8 μm, while the smallest were recorded in *Cassipourea eketensis* which has a mean size of only 14·65 × 5·93 μm. The stomata of all species of *Rhizophora* are distinctly elliptical in outline while they are more or less circular in all species of the remaining genera.

The morphology of the guard cells and their cuticular ledges vary significantly within the family. The rims of some guard cells are heavily cutinized and therefore appear quite distinctive. In all species of *Cassipourea, Anisophyllea* and *Poga*, there is a distinct outer stomatal rim, whereas the rims of *Rhizophora* species are conspicuously two-lipped. Moreover, the cuticle of the common wall between the guard cells of *Anisophyllea sororia* (Fig. 3b), *Anisophyllea purpurascens* and *Poga oleosa* (Fig. 3d) are heavily thickened and they form 'T' pieces at the stomatal poles. These 'T' thickenings are reduced to rods in *Anopyxis klaineana* (Fig. 2e), the only species without any distinct stomatal rim.

Simple, unicellular, tapering trichomes, which usually abscise from the epidermal surface are represented by basal cell scars in *Cassipourea congoensis* (Fig. 1e), *Anisophyllea sororia* (Fig. 3a, b) and *Poga oleosa* (Fig. 3c).

DISCUSSION

The preceding observations and the summaries of character variation in Tables 1 and 2 show that the diversity of epidermal morphology in the Rhizophoraceae has taxonomic applications. The diagnostic value and phylogenetic significance of the various leaf

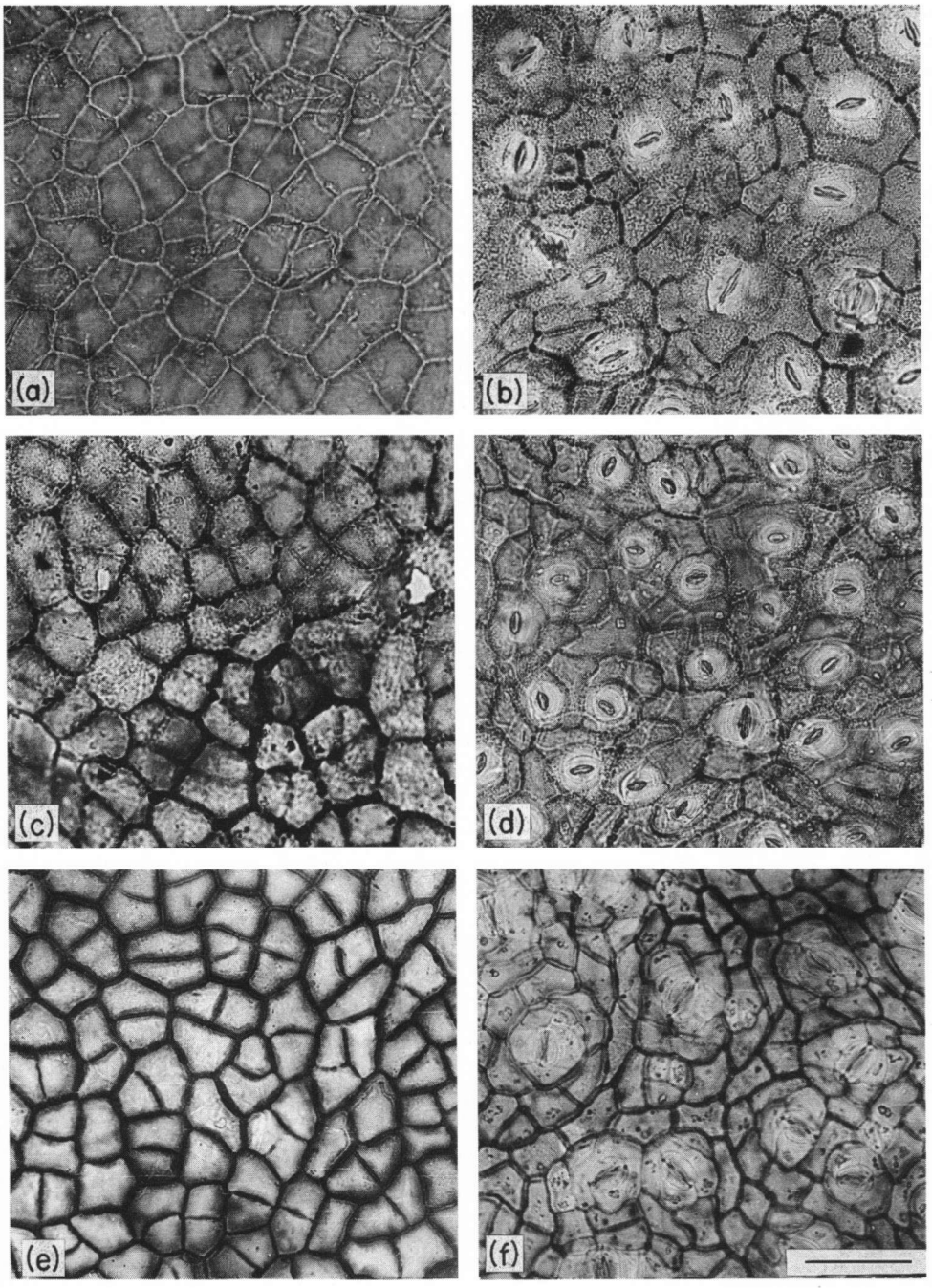

Fig. 2. Adaxial and abaxial epidermal surfaces of *Cassipourea* and *Anopyxis* species. (a) *Cassipourea barteri*, adaxial epidermis. (b) *C. barteri*, abaxial epidermis. (c) *C. gummiflua*, adaxial epidermis. (d) *C. gummiflua*, abaxial epidermis. (e) *Anopyxis klaineana*, adaxial epidermis. (f) *A. klaineana*, abaxial epidermis showing anisocytic stomata. All same scale = 50 μm.

Table 2. Stomatal features of the family Rhizophoraceae

Genera and species	Stomatal type	Stomatal density mm^{-2} min(mean ± SE)max	Stomatal rim	Stomatal size: min(mean ± SE)max (μm) Length	Width
Rhizophora					
racemosa	Cyclocytic	9(11 ± 0·24)13	Double	28·0(33·23 ± 0·72)48·0	11·2(14·0 ± 0·38)16·8
harrisonii	Cyclocytic	8(10 ± 0·26)14	Double	36·4(41·63 ± 0·83)57·4	11·2(12·83 ± 0·21)14·0
mangle	Cyclocytic	6(8 ± 0·23)11	Double	37·8(43·40 ± 0·65)50·4	9·8(12·09 ± 0·24)14·0
Cassipourea					
congoensis	Paracytic	7(20 ± 0·78)40	Single	16·8(20·49 ± 1·29)47·6	16·8(13·59 ± 0·25)25·2
eketensis	Paracytic	11(20 ± 0·97)28	Single	14·0(14·65 ± 0·22)16·8	5·6(5·93 ± 0·11) 7·0
barteri	Paracytic	8(23 ± 0·64)36	Single	16·8(20·0 ± 0·20)23·8	12·6(14·0 ± 0·29)23·8
gummiflua	Paracytic	37(43 ± 1·05)53	Single	14·0(17·55 ± 0·45)22·4	8·4(12·04 ± 0·24)14·0
Anopyxis					
klaineana	Anisocytic	14(29 ± 0·53)35	Indistinct	11·2(14·59 ± 0·37)25·2	4·2(5·79 ± 0·11)11·2
Anisophyllea					
sororia	Paracytic	29(41 ± 0·89)50	Single	15·4(17·27 ± 0·20)19·6	7·0(10·26 ± 0·22)13·8
purpurascens	Paracytic	24(38 ± 0·61)44	Single	16·8(20·0 ± 0·28)23·8	8·4(9·42 ± 0·32)14·0
Poga					
oleosa	Anomocytic	15(16 ± 0·24)24	Single	16·8(28·47 ± 0·60)43·2	11·2(18·57 ± 0·27)24·6

Abbreviations: min, minimum; SE, standard error; max, maximum.

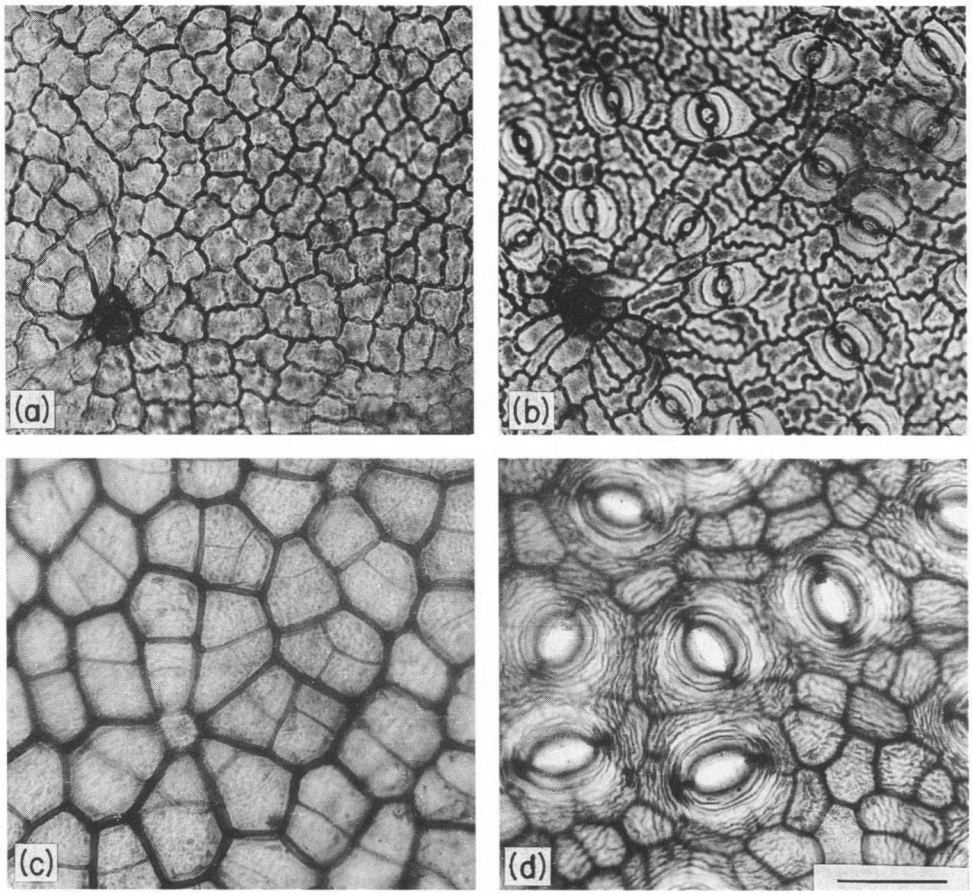

Fig. 3. Adaxial and abaxial epidermal surfaces of *Anisophyllea* and *Poga* species. (a) *Anisophyllea sororia*, adaxial epidermis with undulate anticlinal walls. (b) *A. sororia*, abaxial epidermis showing T-shaped thickenings of stomatal poles and undulate walls. (c) *Poga oleosa*, adaxial epidermis showing secondary anticlinal divisions of the cells. (d) *P. oleosa*, abaxial epidermis with cuticular striations and T-shaped thickenings of stomatal poles. All same scale = 50 μm.

epidermal and cuticular characters in eight genera of mangroves represented in three families, including the Rhizophoraceae, has been demonstrated by Stace (1966).

Evidence obtained in this study supports the suspected hybrid origin of *Rhizophora harrisonii*. Most of the micromorphological characters assessed for this taxon are usually intermediate between those of *R. racemosa* and *R. mangle*, the presumed parents. Breteler (1969, 1977) has shown that *R. harrisonii* is morphologically and ecologically intermediate between the two parental species and also has a high degree of sterility and overlapping geographic range. The hybrid name, *Rhizophora* × *harrisonii* Leechman, is therefore taken to be the correct name of this taxon (Tomlinson 1986).

The presence of a relatively large cyclocytic type of stomata, distinct double stomatal rim and thick-walled cells among other features, in both species of *Rhizophora*, clearly distinguish this genus from other genera in the family. This confirms earlier observations of Marco (1935) and Metcalfe & Chalk (1950), based on wood anatomy, that the Rhizophoreae form a well-defined, homogeneous natural group, which is readily

separable from other members of this or any other family. The cyclocytic subsidiary cells found in *Rhizophora racemosa*, *R.* × *harrisonii* and *R. mangle* are generally thought to be specializations of the anomocytic type. The cyclocytic stomatal type which is restricted to the Rhizophoreae has also been observed and recorded by Keating & Randrianasolo (1988).

Anisophyllea is unique within the family in the possession of undulate cuticular flanges in its two species, *A. sororia* and *A. purpurascens*, the other genera being characterized by either straight or curved anticlinal walls. The effect of light intensity on epidermal wall undulation has long been recognized (Haberlandt 1934; Watson 1942; Stace 1965); it can, however, be used as a supporting diagnostic character provided due caution is taken (Wilkinson 1989). The genus *Anopyxis*, which is placed tentatively with *Cassipourea* in the tribe Macarisiea, differs from the latter in the possession of anisocytic stomata and lack of a distinct stomatal ledge. These features do not support the inclusion of these genera in the same group.

Within the family, the T-shaped cuticle at the stomatal poles of all species of *Anisophyllea* and *Poga* suggests affinity. On the contrary, the undulate anticlinal walls and paracytic stomata of the former separate all its species from the latter which usually has straight or curved walls and anomocytic stomata. Epidermal characters that set these two genera apart therefore outweigh than the ones they have in common. Evidence from this investigation is therefore insufficient to support the placement of these genera in the same separate family (Keay 1989).

Some characteristics of the epidermis are sufficiently distinctive for the clear recognition of certain species within the family. Among the best of these are the striate epidermal walls and secondary anticlinal division of adaxial cells, of *Poga oleosa*; the anisocytic stomata of *Anopyxis klaineana*, as well as the particularly large stomata of *Rhizophora* species. In general, no epidermal feature completely distinguishes the genera *Anisophyllea* and *Poga* which constitute the tribe Anisophylleae, from the remaining genera of the family Rhizophoraceae.

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