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Epidermal Structures and Stomatal Ontogeny in *Terminalia catappa* L. (Combretaceae)

Chimezie Ekeke and Ikechukwu O. Agbagwa
Department of Plant Science and Biotechnology, Faculty of Biological Sciences, University of Port Harcourt, PMB 5323, Port Harcourt, Nigeria

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Corresponding Author:
Ikechukwu O. Agbagwa,
Department of Plant Science and Biotechnology,
Faculty of Biological Sciences,
University of Port Harcourt, PMB 5323,
Port Harcourt, Nigeria

ABSTRACT

Stomatal ontogeny and epidermal characteristics of *Terminalia catappa* L., an important tropical economic plant, were studied and described. The central portions of cotyledonary and mature leaves were peeled, stained with acetocarmin, 1% safranin and fast green stains as required, mounted on microscope slides and observed under Olympus photomicroscope for stomata ontogeny and developmental stages. The cells of the epidermis of the species are polygonal, isodiametric or elongated in various directions and arranged irregularly. The anticlinal epidermal walls are sinuous, undulating, straight or arched. Combretaceous eglandular trichomes were observed on the abaxial surface of the cotelydonary leaves. Six types of stomata (anomocytic, tetracytic, stuarocytic, anisocytic, isotricytic, diacytic) and different transitional stages were also observed. Stomata occurrence in cotyledonary leaves was observed to be amphistomatic but hypostomatic in mature leaves. The adaxial stomatal index on the cotyledonary leaves ranged from 3.57-14.29 (9.61±3.15) while on the abaxial surface it varied from 12.50-31.25 (23.50±5.13). The ontogeny of isotricytic stomata is mesogenous; it is however mesoperigenous in anomocytic, tetracytic and anisocytic stomata types. Stomata clusters are frequent on the abaxial surface of mature leaves while contiguous stomata and abnormal stomata with unequal guard cells are rare. Stomatal ontogeny, an important taxonomic character, is described for the species.

Key words: Combretaceous hairs, epidermis, meristemoid, ontogeny, stomata cluster, *Terminalia catappa*

INTRODUCTION

Terminalia L. belongs to the family Combretaceae. The genus comprises around 100 species distributed within tropical regions. Eight of the eleven *Terminalia* species recorded in tropical West Africa by Hutchinson and Dalziel (1954) occur in Nigeria. The species are small, medium and large deciduous shrubs or trees of 1.5-75 m tall (Schmidt *et al*., 2002). Some of the species have cylindrical boles that are very straight and long with small to large buttresses and sometimes branchless for up to 30 m (Lemmens *et al*., 1995). The genus has several medicinal, economical, spiritual and social values (Irvine, 1961; Srivastava *et al*., 1992; Lemmens *et al*., 1995; Schmidt *et al*., 2002; Smith *et al*., 2004; Satardekar and Deodhar, 2010; Sharma and Mukundan, 2014; Rathinamoorthy and Thilagavathi, 2014). In traditional medicines, derivatives of *Terminalia* species have been used in Africa and Asia (Lawes *et al*., 2004; Steenkamp *et al*., 2004; Moshi and Mbwambo, 2005). Also many species of this genus have been identified as sources of raw materials for pharmaceuticals and cosmetics production (Dalziel and Hutchinson, 1937; Irvine, 1961). Extracts of the flowers, fruits, barks, leaves, stems and roots of *Terminalia catappa* and other members of this genus are used in the treatment of malaria, eczema, gonorrhea, diabetics, leprosy, candidosis, dermatitis, scurfy affection, tuberculosis, kidney and liver diseases (Batawila *et al*., 2005; Masoko *et al*., 2005; Fyhrquist *et al*., 2006; Kamtchouing *et al*., 2006; Gupta, 2012). Different colours of dyes (black, red, orange, yellow and brown) extracted from leaves, fruits, barks and roots of *Terminalia* species are used for different industrial purposes (Dalziel and Hutchinson, 1937; Errington and Chisumpa, 1987). Bark and fruits of *T. catappa* and *T. serice* are important sources of tannin, as well as gum and resins for glazing pottery (Irvine, 1961; Lemmens and Wulijarni-Soetjipto, 1991; Ellery and Ellery, 1997). Also oil extracts from the seeds of *T. catappa* are used as substitute for groundnut, cotton seed and silk cotton seed oils (Irvine, 1961).

Epidermal characteristics in general and ontogeny of stomata in particular have been utilized at different times for taxonomic delimitation of taxa at the genus and family levels (Van Cotthem, 1970; Paliwal *et al*., 1980; Naidu and Shah, 1981; Das, 2002; Agbagwa and Okoli, 2005, 2006; Amaral and Mello-Silva, 2008; Abubakar *et al*., 2011). The number, arrangement, size and shape of subsidiary cells surrounding the guard cells have also proven to be of great taxonomic value in angiosperms (Stace, 1984; Tomlinson, 1974; Esau, 1977; Baranova, 1987; Stebbins and Khush, 1961; Metcalfe and Chalk, 1979; Agbagwa and Okoli, 2005, 2006). Though Ramassamy and Kannabiran (1994) utilized such epidermal characteristics as stomata and trichome types and stomatal ontogeny for taxonomic elucidation of some *Terminalia* species in India, taxonomic studies are lacking in the genus. There is no report on the ontogeny of stomata in *Terminalia catappa*. This study focused on the ontogeny of stomata and epidermal characteristics (stomata and trichomes) of this important species with the aim of increasing taxonomic information for the genus on one hand and the species in particular. It also strived to establish the ontogenic pathways of the different stomatal types in the species.

MATERIALS AND METHODS

Seeds of *Terminalia catappa* were germinated in pots within the experimental garden, Department of Plant Science and Biotechnology, University of Port Harcourt, Nigeria in May 2013. Young cotyledonary leaves at different developmental stages and leaves of mature plants were collected, fixed in FAA for 24 h and thereafter preserved in 70% ethanol. The central portions of cotyledonary and mature leaves were peeled, stained and mounted on No. 1 microscope slides for microscopic observation. Cotyledonary peels were stained with acetocarmin while matured peels were stained with 1% safranin and fast green stains. The slides containing the epidermal peels were critically observed for stomata ontogeny and developmental stages. The epidermal characteristics and trichome types were also recorded. Good microscopic observations were photographed with Cannon A420 digital camera fitted to Olympus photomicroscope and neatly sketched out for clarity.

The terminology of Prabhakar (2004) was used for stomatal classification. These include tetracytic (stoma completely surrounded by only 4 subsidiary cells, variable in size and shape of which two are polar and two are lateral in position), brachyparacytic or anomocytic (stoma completely surrounded by more than four subsidiary cells, variable in size and shape other than tetracytic and stuarocytic types), staurocytic (stoma completely surrounded by only 4 subsidiary cells, variable in size and shape, of which two co-join at the polar and two are lateral to the guard cells), isotricytic (stoma completely surrounded by only 3 subsidiary cells, variable in position and shape but 3 of the subsidiary cells are more or less of equal size), anisocytic (stoma completely surrounded by only 3 subsidiary cells, variable in position and size but one of the subsidiary is distinctly small) and diacyctic (stoma completely surrounded by only 2 distinct or indistinct subsidiary cells which are equal or unequal in size) stomata types. The terminology for stomatal ontogeny was adopted from Pant (1965).

RESULTS

Epidermal characteristics, stomatal types and distribution: In *T. catappa*, the shape of the adaxial epidermal cells in cotyledonary and mature leaves, were observed to be similar in being irregular with undulating anticlinal cell walls (Fig. 1a-l); the abaxial epidermal cells were likewise similar being irregular in shape but straight, wavy or curved anticlinally (Fig. 1m-s). Variation in size was however observed between the cotyledonary and mature leaves. In the mature leaves, the adaxial and abaxial epidermal cells measured 24.38±6.79 µm multiplied by 10.12±2.22 µm and 24.38±3.10 µm multiplied by 14.03±3.33 µm, respectively. The epidermal cells of the cotyledonary leaves are more elongated than those of the mature leaves. They are 38.64±10.16 µm multiplied by 36.11±8.48 µm on the abaxial epidermis and 46.00±8.19 µm multiplied by 23.92±2.91 µm on the adaxial epidermis (Table 1). Eglandular trichome was observed on the abaxial epidermal surface of the cotelydonary leaf (Fig. 1t).

Generally six mature stomata types, transitional stages, contiguous stomata and stomatal clusters were identified in the cotyledonary and mature leaves (Fig. 1a-o, 2a-i). These stomata types are anomocytic (AM), tetracytic (TE), stuarocytic (ST), anisocytic (AS), diacytic (DI) and isotricytic (IT) (Fig. 1a-r). In the cotyledonary leaves, stomata were observed on the adaxial and abaxial epidermis (amphistomatic) while in the mature leaves they occurred only

Table 1: Epidermal and stomatal characteristics of mature and cotyledonary leaves of *T. catappa*

	Guard cell		Subsidiary cell		Epidermal cell	
Leaf age and epidermal layer	Length (µm)	Width (µm)	Length (µm)	Width (µm)	Length (µm)	Width (µm)
Matured leaves						
Lower	14.95±2.24	8.05±1.21	17.71±4.61	9.20±2.17	24.38±6.79	10.12±2.22
Upper	-	-	-	-	24.38±3.10	14.03±3.33
Cotyledonary leaves						
Lower	13.57±1.70	8.28±1.19	23.00±4.60	19.78±3.63	38.64±10.16	36.11±8.48
Upper	16.56±2.61	8.28±1.19	28.29±3.09	25.07±3.98	46.00±8.19	23.92±2.91

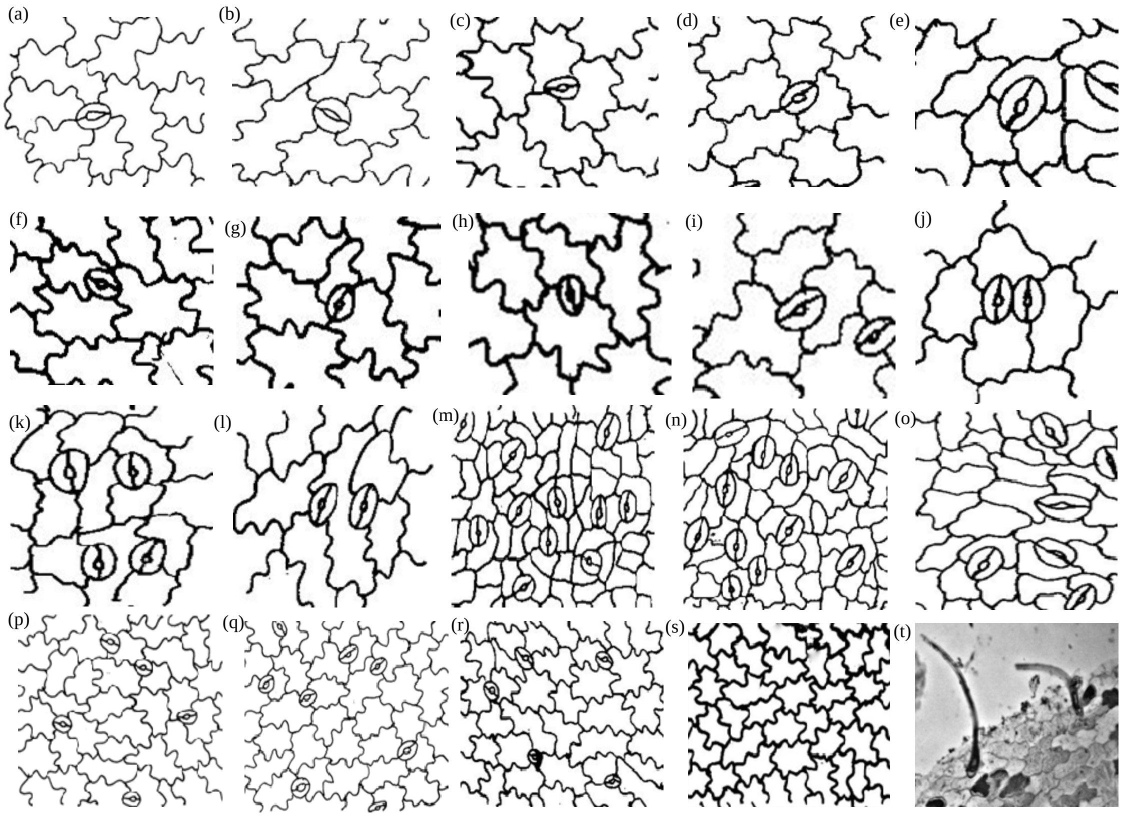

Fig. 1(a-t): Different epidermal and stomatal types, (a) Anomocytic stoma (AM), (b) Tetracytic stoma (TE), (c, e and i) Isotricytic stoma, (d) Staurocytic stoma (ST), (f and g) Anisocytic stoma (AS), (h) Diacytic stoma (DI), (f) Isotricytic stoma (IT), (j-q) Clustering of different stomatal types, (r) AM-AS, (s) Adaxial epidermal peel of mature leaf and (t) Eglandular trichome

Table 2: Summary of stomatal Index (SI) in *Terminalia catappa*

Leaf stage and surface	Range	Mean±SD
Matured leaves		
Upper (adaxial)	-	-
Lower (abaxial)	28.57-38.23	33.23±2.81
Cotyledonary leaves		
Upper (adaxial)	3.57-14.29	9.61±3.15
Lower (abaxial)	12.50-31.25	23.50±5.13

Table 3: Single factor analysis of variance (ANOVA) for the stomatal index on abaxial surfaces of mature and cotyledonary leaves

Source of variation	SS	df	MS	F	p-value	F-crit
Between groups	1101.03	1	1101.03	61.11251	1.98E-09	4.098172
Within groups	684.6251	38	18.01645			
Total	1785.656	39				

on the abaxial epidermis (hypostomatic). Stomata occurred predominantly in the area between leaf veins and sparingly on the leaf veins. Though stomata occurred on the adaxial surface of the cotyledonary leaves, these were not observed on the adaxial surface of mature leaves. The adaxial stomata observed in cotyledonary leaves therefore gradually fade away in the course of leaf development and maturity.

The stomatal index is presented in Table 2. On the cotyledonary leaves, the adaxial stomatal index ranged from 3.57-14.29 (9.61±3.15) while on the abaxial surface it varied from 12.50-31.25 (23.50±5.13). The stomatal index on the abaxial surface of mature leaves varied from 28.57-38.46 (33.24±2.82). There is significant difference between the stomatal index on the abaxial sufaces of the cotyledonary and mature leaves. This is as a result of variation on the stomata density on the cotyledonary leaves (Table 3). This is expected since the cotyledonary leaves are still under developmental processes.

On the epidermis of mature leaves of *T. catappa*, five stomata types were observed. These stomata and cluster types are: Anomocytic (Fig. 1a), tetracytic (Fig. 1b), stuarocytic (Fig. 1d), anisocytic (Fig. 1f, g) and isotricytic (Fig. 1c, e) stomata. Tetracytic, anomocytic and isotricytic stomata were the most dominant types observed. Anisocytic and staurocytic stomata types were rare. Also, stomatal clusters were found in the mature leaf epidermis. The clustering and position of the stomata varied alongside with combination of the different stomata types identified. The different positioning of the stomata is lateral (parallel), adjacent or polar. The clustering of stomata found in this species showed that several stomata may cluster together but comprising of few stomata types. For example, AM-TE-IT (Fig. 1m), TE-AM (Fig. 1n), TE-IT

(Fig. 1o), IT-IT (Fig. 1p) and AM-AS (Fig. 1r) but consisting of three or more stomata. The guard cells in mature *T. catappa* leaves were 14.95±2.24 µm long and 8.05±1.21 µm wide while the subsidiary cells were 17.71±4.61 µm long and 9.20±2.17 µm wide in sizes (Table 1).

Stomatal ontogeny: The meristemoids or stomatal initials are conspicuous and were identified by their small sizes, double wall and deeply stained nature. These were randomly distributed on the leaf surface and sometimes occurred between mature stomata being mostly spherical or oval shaped (Fig. 2). Also some of them were observed to be isodiametric, triangular, rectangular or trapezoid in shape (Fig. 2c-e, j, k and Fig. 3e, h, q, r). The meristemoid may occur singly, in groups of two or more. Where it occurs singly, it gives rise to distinct stoma; however, if they occur in groups they give rise to different stomata types probably clusters or contiguous types (Fig. 1j-q). Except the ontogeny of diacytic and stuarocytic stomata, which were not clear and therefore not presented, the ontogeny of the other stomata types is presented as follows:

- **Isotricytic stomata:** In isotricytic stomata, the meristemoid, M or M_1 (Fig. 3a) enlarges and divides into two unequal cells. The larger cell develops into the first subsidiary cell (S_1) as shown in Fig. 3b while the small Guard Mother Cell (GMC) enlarges and split unequally into two to give the second subsidiary cell (S_2) (Fig. 3c-d). The meristemoid further enlarges and divides unequally to produce the third subsidiary cell (S_3) (Fig. 3e). After this third stage of division, the central meristemoid (GMC) enlarges and divides equally to produce two guard cells which subsequently develop into mature stomata (Fig. 3f). The ontogeny type is known as mesogenous. It is worthy to note that it is the smaller cell that remains meristematic
- **Anisocytic stomata:** The development of anisocytic stomata in the species is mesoperigenous. The meristemoids M_2 (Fig. 4a-b) enlarges and divides unequally into two cells. The larger part of the cells develops to form the first subsidiary cell, S_1 (Fig. 4c) while the smaller cell forms the GMC, grows bigger and divides equally to form the guard cells (Fig. 4d). The cells thicken and grow into the guards cell (Fig. 4e). During this stomatal development, a single subsidiary is produced from the meristemoid and the subsidiary cell does not grow as big as that in isotricytic development (Fig. 1g, f) thereby resulting to anisocytic stomata
- **Anomocytic stomata:** The ontogeny of anomocytic stomata as observed is mesoperigenous. The meristemoid, M4 (Fig. 5a-b) embedded between four epidermal cells

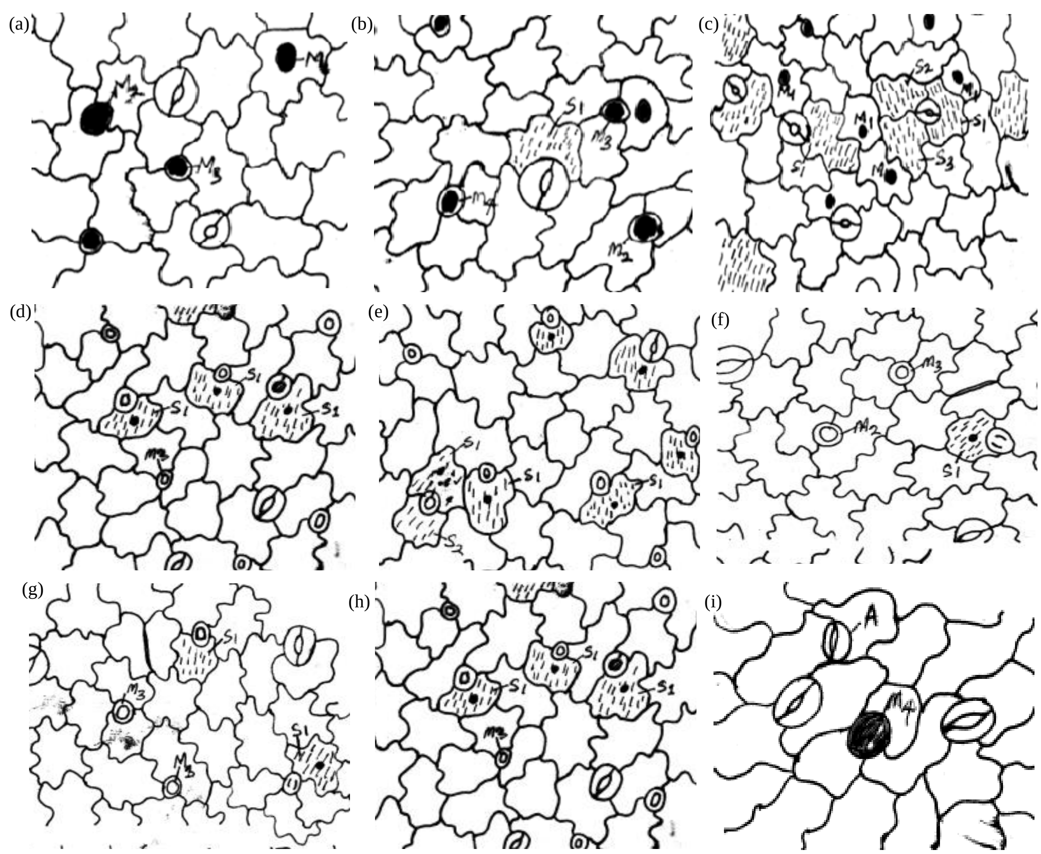

Fig. 2(a-i): Variation in organization of transitional stages of different stomatal developmental types and clusters

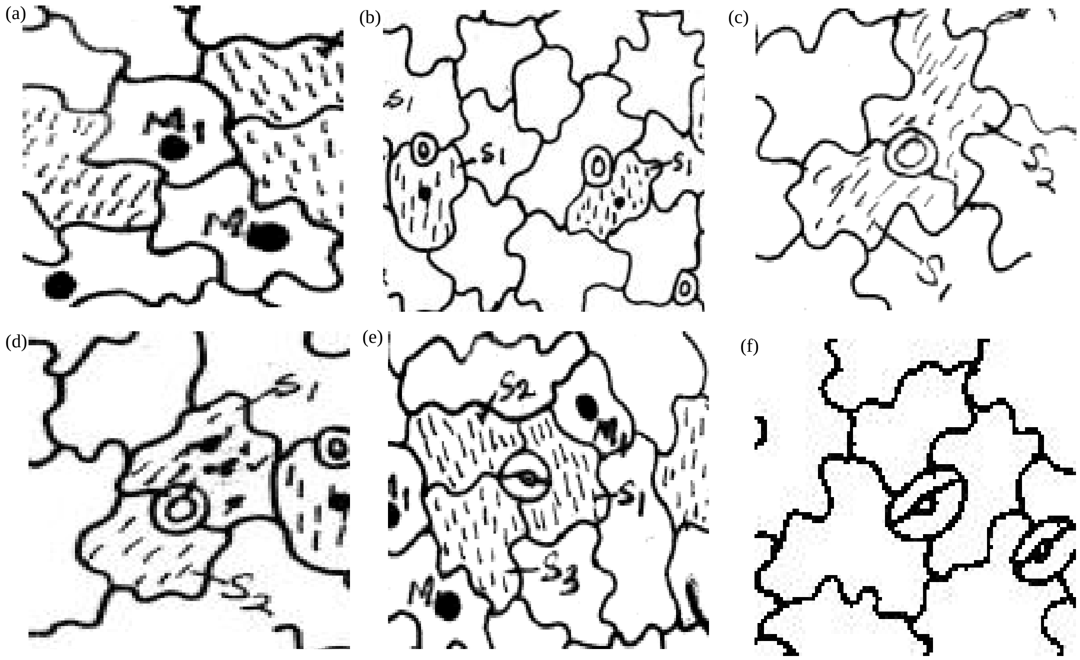

Fig. 3(a-f): Ontogeny of isotricytic stomata, (a) Young meristemoid, (b) Formation of the first subsidiary cell (S_1), (c and d) Formation of the second subsidiary cell (S_2), (e) Formation of the third subsidiary cell (S_3) and (f) Mature isotricytic stoma

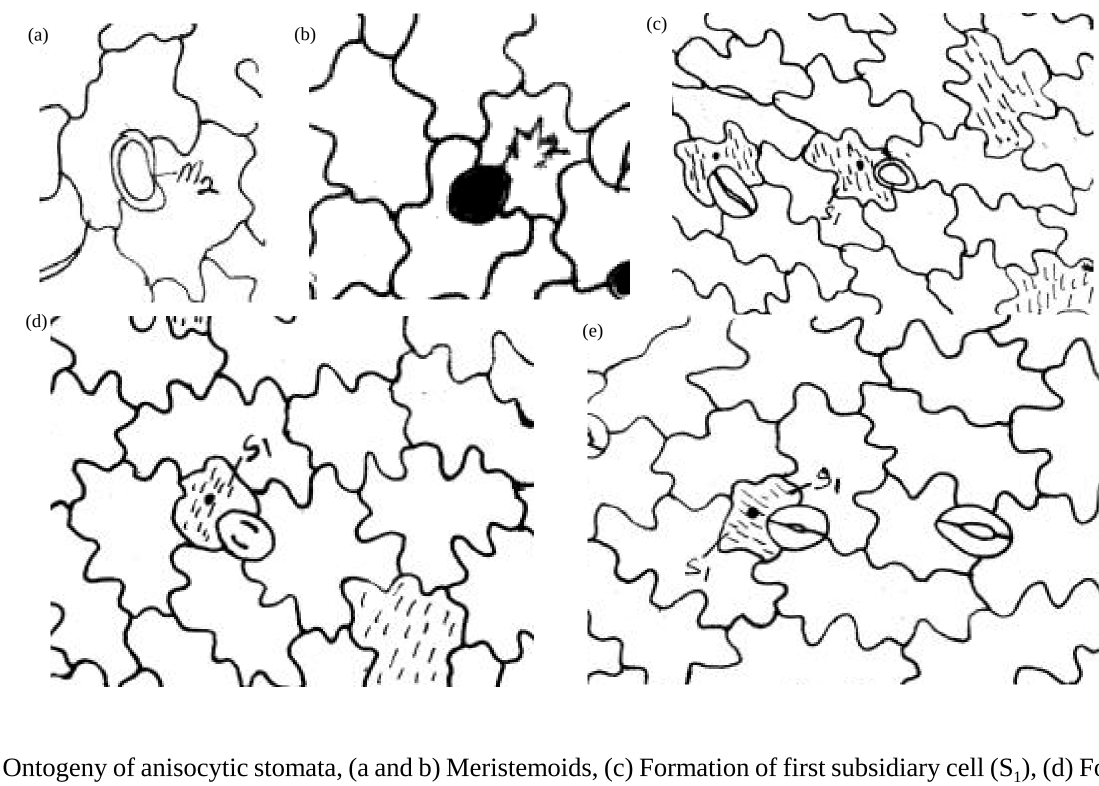

Fig. 4(a-e): Ontogeny of anisocytic stomata, (a and b) Meristemoids, (c) Formation of first subsidiary cell (S_1), (d) Formation of guard cells and (e) Anisocytic stoma with first subsidiary cell (S1)

grows, enlarges in size and divides unequally into two cells. The larger cell develops and become the first subsidiary cell (S1) while the smaller develop into the stomatal guard cells (Fig. 5c) and finally mature stomata

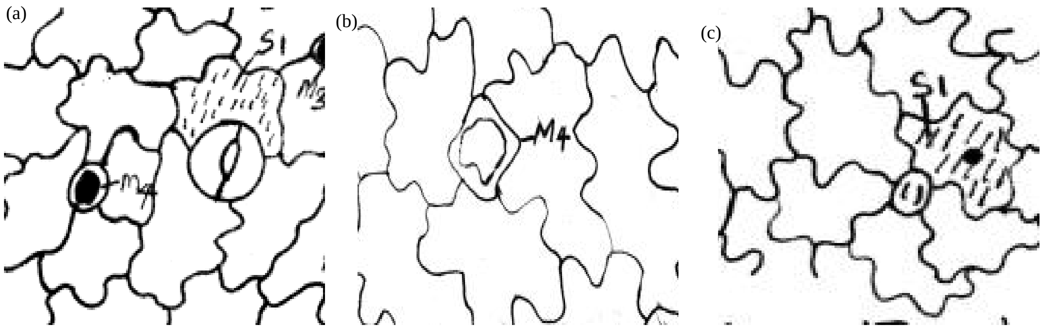

Fig. 5(a-c): Ontogeny of anomocytic stomata, (a and b) Meristemoids (M_4) and (c) Anomocytic stoma with first subsidiary cell (S_1) and developing guard cells

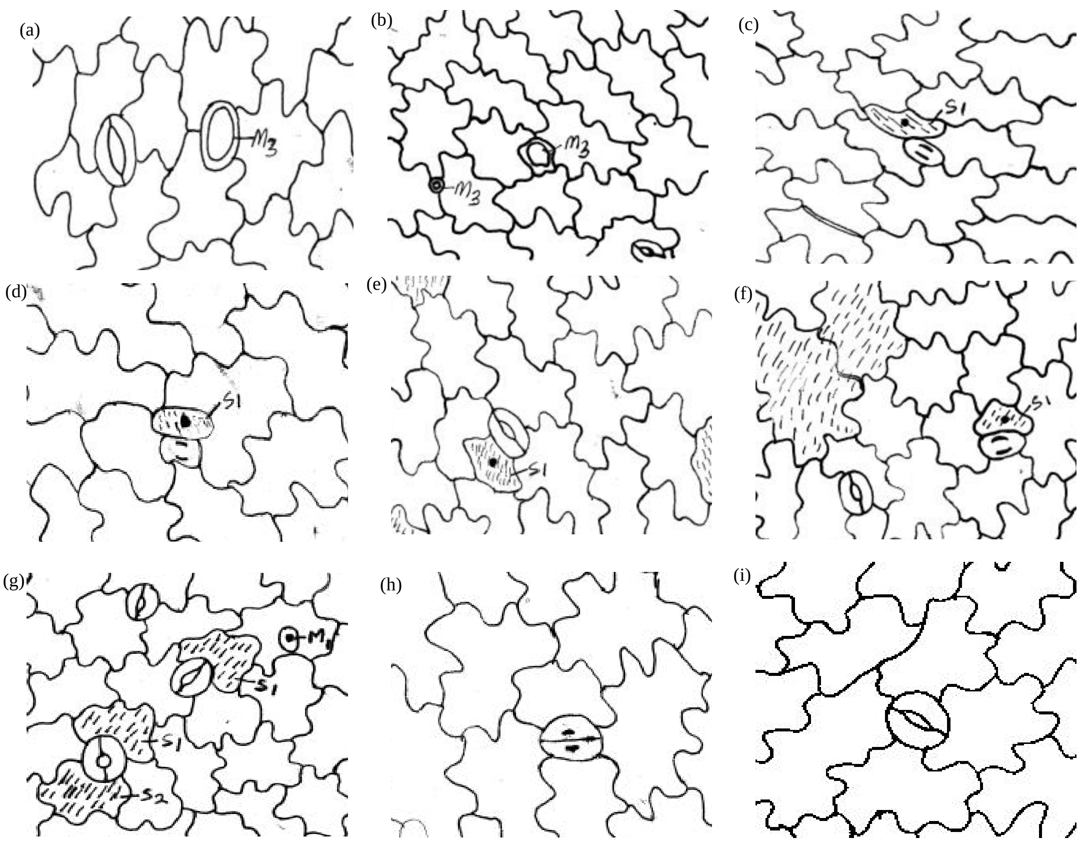

Fig. 6(a-i): Ontogeny of tetracytic stomata, (a and b) Meristemoids M_3 and (c, d, e, f and h) Tetracytic stoma with first subsidiary cell (S_1) and developing guard cells, (g) Tetracyitc stoma with first (S_1) and second (S_2) cells and (i) Matured tetracytic stoma

- **Tetracytic stomata:** The development of this stomata type was observed to be mesoperigenous following two developmental pathways: (1) Similar to anisocytic type the meristemoid M_2 enlarges, divides unequally and give rise to the first subsidiary cell S_1 (Fig. 4c). Thereafter, the smaller cell divides in the opposite side to produce the second subsidiary cell S_2 (Fig. 6g), (2) Meristemoid M_3 (Fig. 6a-b) increases in size and split into two unequal cells to give rise to the first subsidiary cell (S_1) which are of different shapes, sizes and orientation (Fig. 6c-f). Finally, the last stages in step 1 and 2 grow, divide into two equal cell which subsequently give rise to mature stomata as shown in Fig. 6h-i

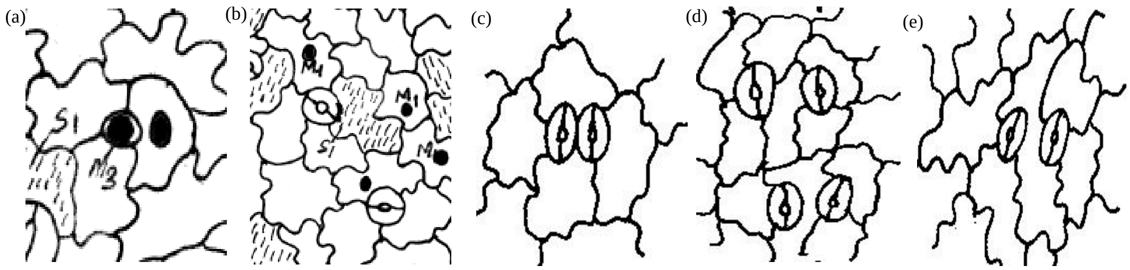

Fig. 7(a-e): Development of contiguous and stomatal cluster, (a) Two adjacent meristemoids, (b) Meristemoids adjacent to mature stomata, (c) Contiguous stomata and (d and e) Stomata cluster or in group

Contiguous stomata and stomatal clusters: Formation of contiguous stomata occurs when two adjacent meristemoids (Fig. 2b-c and 7a-b) or meristemoids adjacent to mature stomata (Fig. 7b) enlarge, divide equally into two guard cells and the guard cells joining each other (Fig. 7c). During formation of stomatal cluster, the meristemoids as shown in Fig. 2 develop and transform into mature stomata of different types. This leads to clustering of different stomata types and combinations (Fig. 1k-r and 7d-e).

Abnormal stomata: These types of stomata arise when the GMC divides unequally to form two guard cells (Fig. 2i).

DISCUSSION

The stomata in the Combretaceae provide many important structural and distributional features, which are of taxonomic value at the species level (Stace, 1965a, b). These include the degree of pattern of thickening of guard cell wall, the size and shape of guard cells in surface view and the degree of sunkenness in the epidermis. Ramassamy and Kannabiran (1994) described the epidermal structure of mature leaves and stomatal development in seven species of *Terminalia* in India. In their report, all the species they studied had unicellular conical non-glandular hairs; anomocytic stomata were of early and late origin while paracytic, anisocytic and tetracytic stomata were of late origin. They also observed that stomatal frequency varied from species to species. It is found to be due to the difference in the nature of placement of wall in the protodermal cell while cutting off the meristemoid. Based on these findings it is suggested that the constancy of the number of cutting faces of the meristemoid is genus-specific while the behaviour of the wall laid down in the protodermal cell is species-specific.

In this present study, the epidermal structure, trichome type and stomatal ontogeny in *Terminalia catappa* Linn. are described. The epidermal cells are polygonal, isodiametric or elongated in various directions and arranged irregularly. The anticlinal epidermal walls are sinuous, undulating, straight or arched. Combretaceous eglandular trichomes were observed on the abaxial epidermal surface of the cotelydonery leaves. Occurrence of different types of stomata (anomocytic, tetracytic, stuarocytic, anisocytic, isotricytic, diacytic), different transitional stomatal stages and different types of stomatal clusters on the same leaf surface were observed in *T. catappa*. The guard cells of mature stomata selected randomly showed variation in size and shape. Occurrence of such type of diversity in stomatal characteristics on one and the same surface has been reported earlier by Metcaife and Chalk (1950) and Shah and Abraham (1981) in Umbelliferae (Apiaceae). Such changes in stomata may be due to diverse stomatal developmental pathways, number of cutting faces, angle of cell division, divisive capacity of meristemoids and subdivisions in the subsidiary cells (Metcaife and Chalk, 1950).

The ontogeny of isotricytic stomata in the species is mesogenous while that of the other three (anomocytic, tetracytic and anisocytic) is mesoperigenous. Groups of stomata are frequent but abnormal stomata with unequal guard cells and contiguous stomata rarely occurred in the species. A combination of different types of mature stomata and such abnormalities have been described by Pant and Kidwai (1964) in *Phylanodiflora*, a member of Verbenaceae and in Umbelliferae (Apiaceae) (Shah and Abraham, 1981). The mesogenous ontogeny observed in the isotricytic stomata where the smaller meristemoid cell remains meristematic has also been previously reported (Pant and Banerji, 1965; Pant and Kidwai, 1967; Paliwal, 1967).

Noraini and Cutler (2009) highlighted the need to use anatomical evidence together with morphological characteristics in species identification. On the other hand, Van Cotthem (1970) posited that stomatal types (a kind of anatomical character) are valuable diagnostic characters in taxonomy but that any conclusion of affinities should be confirmed by ontogenic evidence. The different stomatal types and their ontogenic pathways in *T. catappa*, which have been confined by this study, are valuable diagnostic characters, which stand this species out amongst its relatives previously described by Ramassamy and Kannabiran (1994). These stomatal types and their ontogenies are also major contribution to the taxonomic information of the genus *Terminalia*.

It is worthy to note that the cotyledonary leaves in this species are amphistomatic while the mature leaves are hypostomatic. Also that diacytic stomata were found only on the adaxial surface of the cotyledonary leaves but not found on the mature leaves. The phenomenon surrounding the occurrence of stomata on the adaxial surface of the cotyledonary leaves and their disappearance on the adaxial surface of the mature leaves is yet to be understood but certainly constitute important diagnostic information for *T. catappa*. This however underscores the need for developmental studies (anatomy, morphology) in comparative and systematic studies as possible ways of tracking important but ephemeral diagnostic characters. The taxonomic information (occurrence of stomata on the adaxial surface of the cotyledonary leaves and their disappearance on mature leaves) is therefore reported for the first time in this species.

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